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ON THE SIGNIFICANCE OF LIPIDS IN ANTARCTIC ZOOPLANKTON

By

Wilhelm Hagen

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1 INTRODUCTION (5)

1.1 Major Functions of Lipids

What are lipids? Often, they are considered the same as fats. Actually, lipids encompass a most heterogeneous group of substances, from simple hydrocarbons, long-chain alcohols and fatty acids, through fats and waxes to complex phospho- and glycolipids (KARLSON, 1980). Fats (triglycerides) are thus only one -- albeit important -- subgroup of the lipids. Contrary to the proteins and carbohydrates, lipids are defined in terms of their physical characteristics, in particular of their solubility. They are insoluble in water, where, at most, they form emulsions, but are well soluble in nonpolar solvents, their degree of hydrophobia depending greatly on their respective polarities.

It is because of their physico-chemical characteristics that lipids fulfill, in living organisms, a multiplicity of vital roles which proteins and carbohydrates can not fill. HADLEY (1985) gives a golbal overview of these varied functions: phospholipids, for instance, because of their amphoteric nature, both polar and nonpolar, form the skeleton of biomembranes into which, in turn, proteins are embedded ("fluid mosaic model"). These phospholipids, in cooperation with proteins, are responsible for the exchange of nutrients and metabolic products; for information processing (via hormone receptors); for energy transport in mitochondria and chloroplasts (via ATP). Lipids also have a cardinal role in transmission

of nerve impulses: rapid, space- and energy saving "saltatory conduction of impulses" by the vertebrate axon is made possible by insulating properties of the lipid-rich myelin sheath. Lipids are responsible for fascinating feats of biocommunication: the minutest amounts of insect pheromones are perceived over great distances; a mixture of lipids in the head of the whale makes it possible for whales to echolocate invisible obstacles or prey, and to communicate with one another over hundreds of nautical miles (SCHMIDT-NIELSEN 1983).

For pelagic animals -- from copepods to whales - the low density of lipids, which varies according to the lipid class (in ascending order of density: hydrocarbons - wax esters - triglycerides - cholesterol), is of special significance. Lipids confer buoyancy on pelagic animals, which can thus economize locomotor energy while remaining afloat. The sperm whale can even adjust its buoyancy according to the requirements of a dive, by adjusting the density of the lipids in its spermaceti organ through complex heat-exchange mechanisms: during descent, spermaceti oil is cooled and becomes denser than water; for ascent, warming the oil reduces its density. At depth, the sperm whale adjusts buoyancy to that of ambient water density, and so can lie motionless in ambush for its prey, the squid (CLARKE 1978). The relatively slight compressibility and thermal expansion of lipids is of advantage to plankton during vertical migrations. According to SARGENT et al. (1976) ascent of a wax ester-rich copepod from great depths causes only a harmlessly small increase in volume. Furthermore, hydrophobic lipid stores prevent problems due to osmolarity (SARGENT 1976), while lipid metabolism produces water that does not

of
participate in the processes/osmosis ("osmosis independent water") (HOCHACHKA and SOMERO 1980).

In what follows, we shall briefly describe the special significance of lipids for animals of the polar regions. In extreme cold, the functioning of biomembranes is maintained by, among other factors, an increase in the unsaturated fatty acids fraction, which maintains membrane fluidity of poikilothermic animals (and plants) even in below-freezing temperatures (CLARKE 1983). An important prerequisite for survival in polar regions is the ability to store energy in the (6)
form of lipids. This role is filled by the rapidly mobilized lipids, because of their high energy content and low density, better than by proteins and hydrocarbons. (If the lipids of an adult human were replaced with glycogen of the same energy content, body weight would be increased, according to LEHNINGER (1983) by 60 kg). The polar whales and seals are classic examples of the accumulation of massive fat stores (blubber) to survive times of starvation or nurturing. Emperor penguin males prepare for a nearly four months-long period of starvation during the extremes of antarctic climate by laying down large fat reserves. During this period of incubation, they lose nearly 40% of body weight (SCHMIDT-NIELSEN 1983). Warm blooded animals of polar regions -- particularly in the sea -- also benefit from the outstanding insulating properties of layers of fat in which, contrary to fur, thermal exchange can be well regulated by control of the circulation (SCHMIDT-NIELSEN 1983). In mammals, furthermore, particularly hibernating ones, well vascularized brown fat, can produce heat directly from fat stores when hypothermia threatens.

1.2 Lipid Studies of Polar Plankton

Toward the end of the 19th Century, marine biologists at Kiel, such as HENSEN (1887) and BRANDT (1898) were the first to recognize the importance of the chemnical composition of plankton for assessing productivity of a marine area, i.e. for "energy transfer" within a trophic chain:

> "Because even those plankton-eaters which are provided with structures that allow only organisms of a specified size to enter the digestive system usually consume a mixture of vegetable and animal matter, it is obviously of interest to study more closely, not only the total plankton of a given region, but also typical representatives of the most prevalent plankton groups, for both nutrient value and chemical compositon, and to compare these both qualitatively and quantitatively to nutrients produced on land" (BRANDT 1898).

BRANDT and his collaborators were pioneers of marine chemistry and adapted the analytical methods developed by LIEBIG for agricultural chemistry to their plankton research. Even though BRANDT had published the first analyses of Baltic plankton in 1898, ecological investigation of the chemical composition of plankton progressed but slowly up to the 1950s ((ROSENFELD 1904; BRANDT and RABEN 1919/20; WIMPENNY 1919; KLEM 1932; MARSHALL et al. 1934; ORR 1934a,b; GUNTHER 1934; COLLIN et al. 1934; LOVERN 1935: GILLAM et al. 1939; KREY 1950; BAALSRUD 1955). These first studies often used mixed plankton samples which made it difficult to evaluate the data.

Since then, understanding of the chemical composition and correlated biochemical processes of planktons from the middle and lower

latitudes has generally much increased because of greater research activities and modern analytical procedures (LOVERN 1964; GIESE 1966; LAWRENCE 1976; SARGENT 1976), but similar information on polar plankton is lacking. Even though krill has long been recognized as a fat-rich food for whales (LEXOW 1921; KLEM 1932), it was only in 1953 that SHEARD found that the lipid content of Euphausiaceae increased with decreasing water temperature. He was first to establish that the lipid contents of the (formalin fixed) antarctic plankton species, Euphausia superba and Thysanoessa macrura, measured 10-15% of body volume, and to discuss the possible significance of such large lipid fractions for growth and development. MacGINTIE (1955) reports on the (7) large lipid stores in the benthic amphipods near Alaska, and is the first to speculate on the usefulness of such reserves for overwintering and reproduction. LITTLEPAGE (1964) was the first to study the seasonal changes in the lipid contents of zooplankton from the high Antarctic. He finds that the carnivorous copepod, Euchaeta antarctica has generally high lipid contents, which further increase in winter during oogenesis, whereas the herbivorous species, Euphausia crystallorophias, accumulates lipids during the summer, then lives from them in winter. ANDREWS (1966) gives a qualitative description of the size of the oil sacs in fixed specimens of Calanoides acutus, an antarctic copepod, and finds distinct seasoanl variations, mainly among copepodids IV and V.

Marine lipid research received new impetus during the 70s mainly because of the work of LEE and his collaborators (e.g. LEE 1974a,b; LEE et al. 1970a,b; 1971a,b; 1974; LEE and HIROTA 1973). They found

high lipid levels in zooplankton from temperate and polar latitudes and from the bathypelagium and determined that the lipid stores of these animals -- particularly of copepods -- often consist of wax esters; tropical and subtropical zooplankton, on the other hand, has little lipid content. From these findings, LEE and HIROTA (1973) hypothesize that plankton from temperate and polar regions and from the bathypelagium can withstand long periods of inanition with the help of lipid reserves that are often wax esters, while tropical and subtropical planktons have a year-round low-level supply of nutrients available, and thus do not need to accumulate lipid reserves. This hypothesis was later supported by much additional research and has now become widely recognized (BAMSTEDT 1986).

Using copepods as an example, BAMSTEDT (1986) postulated that differences in lipid accumulation reflect different "reproductive strategies", so that as much as possible of the nutrient energy acquired can be used for producing offspring. In the oligotrophic tropics with their high rates of growth, this means short reproductive cycles without accumulation of reserves. In polar regions, on the other hand, slow growth rates and long reproductive cycles predominate. Excess nutrients abounding during spring and summer are stored as lipids and later become available -- independently of nutrient levels -- for reproduction (see also SARGENT et al. 1981).

LITTLEPAGE (1964) warns against generalizations, because lipid storage is a highly complex process, affected by many ecological and

physiological factors (e.g. seasonal cyclicity, type of nutrition, life style, reproduction, metabolic activity). A considerable number of polar zooplankton species (coelenterates, polychaetes, salps), in fact, contain little lipid. LAWRENCE (1976) gives a general overview of the various lipid accumulating mechanisms of marine invertebrates. Why lipids are often stored as wax esters -- in calanoid copepods nearly exclusively -- remains to be satisfactorily clarified. SARGENT (1976; 1978) surmises that wax esters are most suitable for rapid accumulation of large lipid stores because the enzymic regulatory mechanisms, which normally regulate and inhibit lipidogenesis, may be ineffective (SARGENT and HENDERSON 1986).

CLARKE (1983), in an extensive review of the literature, summarizes current knowledge of the physiology and biochemistry of the poikilotherm inhabitants of the polar seas, and also provides a detailed discussion of arctic and antarctic lipid studies (arctic plankton: IKEDA 1972; LEE 1975; PERCY and FIFE 1981; SARGENT and FALK-PETERSEN 1981; antarctic plankton: LITTLEPAGE 1964; BOTTINO 1975; CLARKE [unpublished]). CLARKE'S main point is that the dominant factor to which poikilothermes had to adapt was not low temperature, but extreme seasonality. In addition, CLARKE (1984a) and CLARKE and HOLMES (1986) published personal studies of the lipid composition of antarctic macrozooplankton. REINHARDT and VAN VLEET (1986) are the first to publish a lipid analysis of a zooplankton-fish community of the Antarctic Peninsula. They also attempt to use "marker lipids" (SARGENT and WHITTLE 1981) -- characteristic hydrocarbons or fatty acids moving unaltered through the trophic chain -- to demonstrate

(8)

trophic interactions, and supplement these with studies of food intake. Important contributions came especially from FALK-PETERSEN et al. (1981; 1982; 1987), HOPKINS et al. (1984b; 1985; 1986) and SARGENT et al. (1985), working in a fjord in northern Norway. Of major concern was the elucidation of: population dynamics of the common plankton organisms, reproductive cycles, elaboration of the trophic network, energy transfer and seasonal processes. Lipid metabolism of pelagic organisms is an important aspect of these studies and has contributed greatly to understanding the "arctic fjord" ecosystem.

Analyses as all-encompassing as those of the northern Norwegian Balsfjord (70° N) are not extant from the Antarctic. Current knowledge of lipid metabolism in antarctic plankton species -- excepting commercially important krill (e.g. CLARKE 1980; 1984b; ELLINGSEN 1982; BACHLER 1984) -- are quite incomplete. Winter month-studies are nearly entirely lacking. For many species, only total lipid contents are known, often without data on either individual variances or on the important biological parameters (developmental stage, sex, etc...) necessary for proper interpretation. Such data allow only the broadest generalisations.

BOYSEN-ENNEN (1987) and PIATKOWSKI (1987) only recently completed a zoogeographic characterization of the Antarctic Peninsula and Weddell Sea. Their census forms a solid base for understanding the antarctic pelagic system, but has introduced a plethora of new questions and problems about the system's operation and components.

Many biochemical and physiological adaptations are closely linked to the extreme conditions of antarctic life: in spite of constantly low temperatures, the Antarctic is characterized by a well-marked seasonality of light and ice conditions (e.g. KNOX 1970; NEMOTO and HARRISON 1981) generating an intense, though short period of primary production (EL-SAYED 1970; WHITAKER 1982) as their most prolonged biogical effect. Particularly herbivorous zooplankton has to make optimal use of this short-lived phytoplankton bloom. The organism needs energy for its metabolism and growth, but must also accumulate long-term reserves to survive the oligotrophic antarctic winter, and to reproduce. Whether herbivorous zooplankton in the winter uses other sources of nurtients (ice algae, detritus, etc...) is -- except for krill -- largely unknown. A key question for understanding the antarctic pelagic ecosystem concerns the manner in which zooplankton at the lower end of the trophic chain have adapted through evolution to the extreme seasonality of the south polar seas. If herbivorous antarctic zooplankton actually exploits the intense primary productivity of summer by accumulating long-term energy reserves, this should be reflected in the manner in which these animals regulate lipids.

1.3 Purpose of the Investigation (9)

It was the purpose of the present investigation to use global qualitative and quantitative data on the lipids of zooplankton from the Antarctic Peninsula (spring, summer) and Weddell Sea (summer) to further our understanding of the ecophysiological adaptations to

life in Antractica. Supplemented by important biological data (e.g. developmental stage, sex, length, wet- and dry weights, abundance, primary productivity) the findings concerning lipid content and composition can help in answering a number of discrete questions, which can be subdivided into two large groups:

Ontogeny: are lipid content and composition affected by differences between developmental stages, sexes and specific lengths and weights? Which developmental stages are most endangered by oligotrophic conditions because of minimal lipid reserves? How long can these developmental stages survive from their own lipid reserves?

Seasonality: is it possible to detect seasonal changes in the plankton's lipid contents within the period of observation? How is this refelcted in the lipid composition? Are lipid reserves used for gonadogenesis or as a winter ration? Is lipid storage dependent on the organism's position in the trophic chain? Do schedules of lipid accumulation differ between species that compete with one another in the food chain? What classes of lipids are stored preferentially? Do polar calanoid copepods always lay down their lipid reserves as wax esters (LEE and HIROTA 1973)? Do the Euphausiaceae also lay down reserves in the form of phospholipids, as ELLINGSEN (1982) postulates? Which phospholipids are involved here? To what extend do other plankton taxa accumulate lipids? Are such accumulations primarily wax esters or triglycerides? Is this due to evolutionary adaptation, or to the type of food available?

In answering these questions, the present study focusses primarily on copepods and Euphausiacea, which make up the major fraction of the antarctic zooplankton biomass. In both of these groups it is easy to classify individuals by developmental stage or size, so that ontogenic factors can also be considered. Most copepods and Euphausiaceae in this report are filter feeders, and thus depend upon seasonal primary production, the effect of which on the consumers' lipid metabolism we are investigating. In addition, we include data on the lipids of various other zooplankton species, from different taxa and trophic levels, which are important components in the trophic chain of the South Polar Sea, but the lipids of which have so far not been studied.

2 MATERIALS AND METHODS (10)

2.1 Sample Collection

Samples for the lipid studies were collected during two expeditions of R/V "Polarstern". The ANT II/2 expedition was in a region off the Antarctic Peninsula, where "Polarstern" covered a dense network of collecting stations from 23.10 to 10.11.1983 (southern spring), and at the approximate latitudes 60° to 64° S. (Fig. 2.1; SIEGEL 1986). The principal aim of the expedition was the study of the krill, Euphausia superba, according to the relevant SIBEX (Second International BIOMASS Experiment) agreements. FÜTTERER (1984) has published an exhaustive description of the ANT II/2 expedition, with contributions to the various scientific disciplines from the participants.

During the ANT III/3 expedition from 6.1 to 28.2.85 (southern summer; Fig. 2.2), early work was at a few stations northeast of the Antarctic Peninsula, between the South Shetland and South Orkney Islands (Fig. 2.3). The main study site, however, was the southeastern Weddell Sea, to about 78° S. The expedition's plan included two narrow collecting networks (Boxes) off Vestkapp (Figs. 2.4 and 2.6), worked at an interval of about three weeks in order to document temporal changes in zooplankton. Between the two boxes, "Polarstern" made studies in the southern Weddell Sea (Filchner Depression/Gould Bay, Fig. 2.5). HEMPEL (1985a) has published a detailed report of this expedition, with contributions from participants and a list of station data.

Samples of the ANT II/2 expedition were collected with RMT-1"Rectangular Midwater Trawls" (RMT 1+8; BAKER et al. 1973) and with Bongo and vertical nets. The RMT 1+8 consists of two nets, arranged one over the other. RMT 1 has a mouth of about 1 m^2 and mesh of 320 µm; RMT's 8 mouth measures about 8 m^2, and its mesh 4.5 mm. These double nets were dropped, closed, to a maximal depth of 200 m, then opened by hydroacoustics, and hauled up at a rate of about 0.3 m/s; trawling rate was about 2.5 to 3 knots. The Bongo net (60 cm diameter; 335 µm mesh) was used for double oblique hauls at a maximum depth of 200 m, with lowering/raising rates of about 0.3 to 0.5 m/s, at a trawling rate of about 2 knots. The automatically closing net had a diameter of 70 cm and a mesh of 200 µm and was lowered and raised at rates of 0.5 m/s and 0.3 m/s, respectively.

During the ANT III/3 expedition, samples were collected mainly with a Bongo net (300 µm, 500 µm mesh) and a multiple-closure RMT 1+8M. The RMT 1+8M (ROE and SHALE 1979) consists of three pairs of nets, so that it can be used to collect serially at three pre-planned levels in the water column, which the simple RMT can not do; opening and closing of each net is controlled from shipboard. A few specimens came from ring trawls (1.2 m diameter, 1 mm mesh, double oblique haul), multinet (5-fold vertically closing net; mouth 0.25 m^2 , 100 µm and 200 µm mesh) and krill nets (pelagic trawl; mouth 10 x 10 m, mesh at the bottom: 1mm).

Figure 2.1. Trawling Sites of Expedition ANT II/2 from 23.10 to 10.11.1983 (SIEGEL 1986) (11)

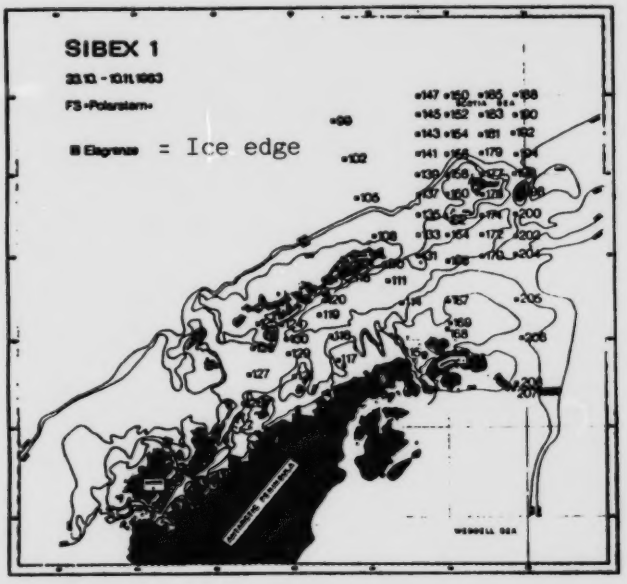


Figure 2.2. Course and Trawl Site Map of "Polarstern" Expedition ANT III/3 (For Boxes I through IV see Figs. 2.3 to 2.6) (HEMPEL 1985a)

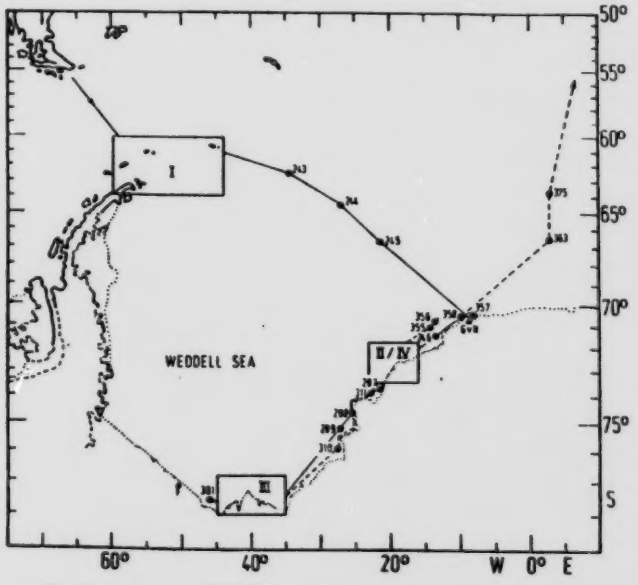


Figure 2.3. Trawl Sites in Study Area I, 6.1. to 13.1.85 (12)
(HEMPEL 1985a)

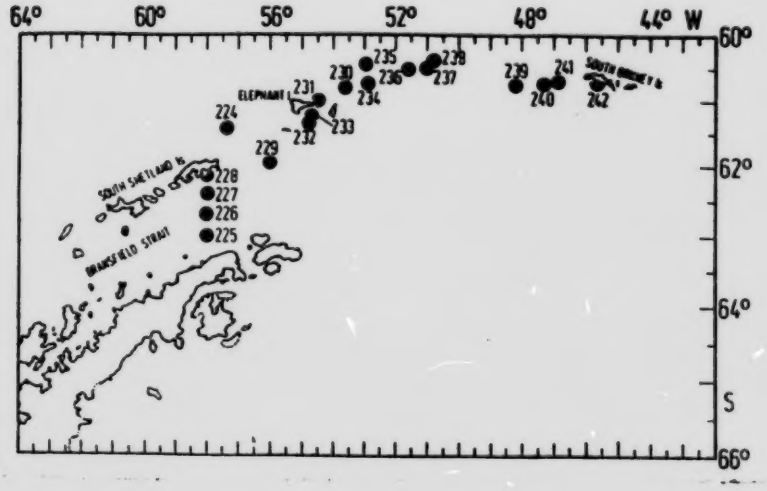


Figure 2.4. Trawl Sites in Study Area II, 22.1. to 1.2.85
(HEMPEL 1985a)

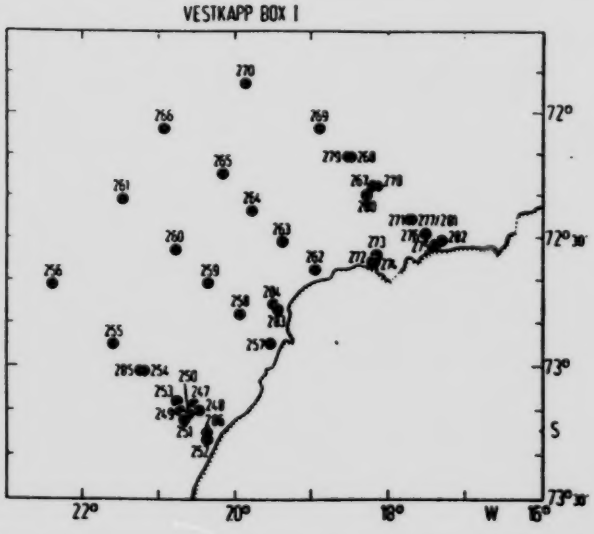


Figure 2.5. Trawl Sites in Study Area III, 2.2. to 9.2.85 -13-
(HEMPEL 1985a)

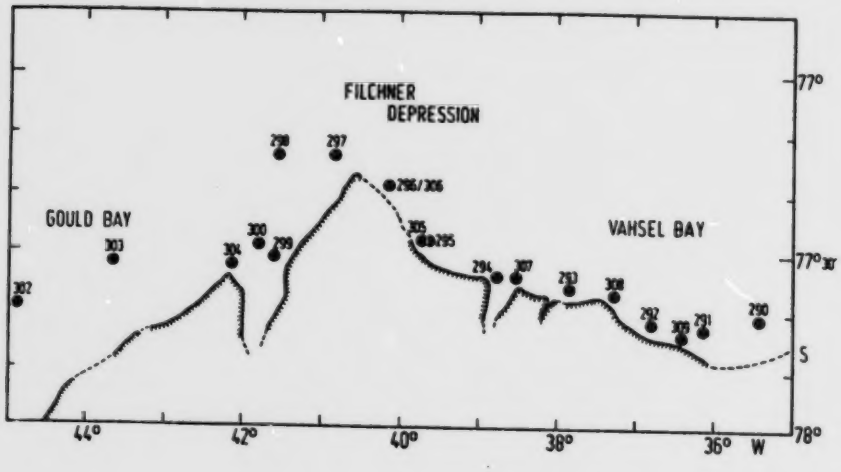
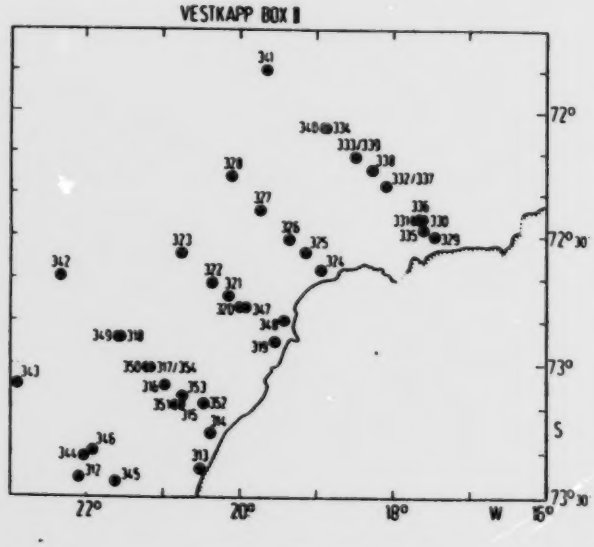


Figure 2.6. Trawl Sites in Study Area IV, 11.2 to 21.2.85
(HEMPEL 1985a)



2.2 Shipboard Processing of Specimens (14)

Immediately after catching, samples (zooplankton, fish larvae, fish) were placed in pre-cooled (0°C) sea water in vats or pails and taken for further sorting to the cold room (approximately 4°C), to prevent autoxydation of the lipids. Whenever possible, only living animals were used for analysis. When specimens were from rare or sensitive species, which could not be kept alive after the haul, special care was taken to select only intact, non-denatured animals (without whitish discolouration of the muscles) for freezing before analysis. In addition to species, we recorded length and, when possible, sex and developmental stage. We were helped in the speciation by Mrs. Midzdalski, a technician trained in taxonomy, who also staged the copepod and euphausid larvae, using a binocular microscope (M5 Wild Co.). For taxonomic problems (Gammaridae, Mysidaceae), duplicates of frozen samples were formalin fixed for later speciation by experts. The specimens were individually cleaned and rinsed in filtered sea water, dried on filter paper and blast-frozen at -80°C in snap-top containers, in which the air (during ANT III/3) had been replaced by nitrogen to prevent oxidation. Copepods and the larvae of Euphausiaceae and fishes, too delicate to dry on filter paper, were carefully transferred to the containers with spring-steel jeweller's forceps, after which sea water was removed with a Pasteur pipette. If the specimens were very small, as many as possible were combined into a single sample (e.g. 400 calyptopis; 200 copepodids; 50-100 fish

larvae), in order to have enough material for weighing the lipids and to offset individual variations.

Table 2.1. List of Species and Developmental Stages Examined

(Weibchen = female; Männchen = male;
Oberglocke = upper bell; Unterglocke = lower bell

COPEPODA
Calanus propinquus C2, C3, C5, F, M
Calanoides acutus C5, F
Rhincalanus gigas C3, C4, C5, F
Metridia gerlachei C4, C5, F
Euchaeta antarctica, sp. C3, C4, C5, F, M
Euchirella rostromagna F
(C= Copepodit-Stadium, F= Weibchen, M= Männchen)

EUPHAUSIACEA
Euphausia superba C1, C2, juv., subadult, adult (F, M)
Euphausia crystallorophias C1-3, C2-3, C3, F1, juv., subadult, adult
Thysanoessa macrura F1-2, juv., subadult, adult
(C= Calyptopis, F1= Furcilie 1; F= Weibchen)

AMPHIPODA
Orchomene sp. (*plebs*, *rossi*)
Epimeriella macronyx
Eusirus propeperdentatus
Eusirus microps
Hyperiella sp. (*macronyx*, *dilatata*)
Hyperia macrocephala
Themisto gaudichaudii
Primno macropa
Vibilia sp. (*propinqua*)
Cyllopus lucasii, sp.
Uristes gigas
Tryphosella cf. *longitelson*
Cyphocaris richardi

MYSIDACEA
Antarctomysis ohlini juv., adult, F
(F=Weibchen)

DECAPODA
Acanthephyra pelagica larv., juv.

COELENTERATA
Calycopsis borchgrevinki
Diphyes antarctica Oberglocken, Unterglocken
Pyrostephos vanhoeffeni
Ctenophora indet.

GASTROPODA
Lamellariidae-Larven
Limacina helicina
Clione limacina
Clio pyramidata

CEPHALOPODA
Galiteuthis glacialis juv.

POLYCHAETA
Vanadis antarctica
Tomopteris carpenteri

CHAETOGNATHA
Sagitta gazellae
Sagitta marri
Eukrohnia hamata

TUNICATA
Salpa thompsoni

PISCES
Notothenia larseni postlarv.
Trematomus eulepidotus juv.
Pleuragramma antarcticum postlarv., juv.

2.3 Laboratory Studies (16)

2.3.1 Determination of Wet and Dry Weights

Weighing was done with a SARTORIUS 1712 MP8 electronic analytical balance (±0.02 mg). For wet weights (w.w.) we used tared, closed glass containers (SUPELCO). In order to prevent the frozen specimens from thawing the containers were kept immersed in liquid nitrogen (-196 C) both before and after weighing. Artefacts that might vitiate results were corrected by weighing empty containers and making suitable adjustments. We used the lowest weights recorded, before condensation could settle on the glass. After obtaining the wet weight, specimens were gently dehydrated for at least 48 hr in a CHRIST ALPHA dry-freezer, and then immediately weighed in the closed containers. The balance needed 15 sec to reach equilibrium; readings were always taken at 30 sec. Again, empty containers were similarly treated, to adjust for effects of temperature and atmospheric pressure on weight. This made it possible to correct dry weight for changes in tare weights taken before and after freeze-drying. Before extracting the lipids, specimens were briefly stored at -80° C.

2.3.2 Measurement of Total Lipid Content

Total lipid is defined as the fraction of lipid that can be extracted from a specimen. Chloroform and methanol are the usual universal solvents. Lipid content is the weight fraction, in percent, calculated on the basis of either wet or dry weight (= 100%).

Currently, two procedures for determining total lipids are used: the sulfophosphovanillin method (SPVM) of ZÖLLNER and KIRSCH (1962) or BARNES and BLACKSTOCK (1973), and the gravimetric method of FOLCH et al. (1957) or BLIGH and DYER (1959). The SPVM is a photometric procedure, which requires only small amounts of lipid, but has the disadvantage that identical quantities of lipids of different classes (phospholipids, triglycerides, waxes, etc...) yield different extinction values because the colour reaction depends on the presence of simple double bonds in the lipids (ZOLLNER and KIRSCH 1962). For species that differ in their lipid compositions, therefore, the extinction values must be carefully calibrated by the use of known quantities of lipid.

According to CHRISTIE (1982) the method of FOLCH et al. (1957) extracts 95-99% of the lipids from tissues (SPVM: 95%). Gangliosides and an occasional glycolipid may be lost with the aqueous phase. HOPKINS et al. (1984a), in connection with their protein determinations, extensively studied potential sources of error when lipids are extracted according to FOLCH et al. (1957). These authors give valuable hints for avoiding artefacts.

The gravimetric method of BLIGH and DRYER (1959) is used when there is much tissue (> 1 g), because it uses less solvent. For our total lipid determinations, I adapted the method of FOLCH et al. (1957). The specimen is coarsely broken up in a pre-cooled Potter homogenizer with a spatula; 5 mL of chloroform/methanol (Nanograde) 2:1 (v/v), with 0.01% butylhydroxytoluol (BHT) antioxidant, are added.

Figure 2.7. Lipid Extraction Scheme (17)

FLOW DIAGRAM

Specimen (dry-frozen)

↓

Potter homogenizer, break up tissues coarsely with spatula

↓

Add 5 mL chloroform/methanol (+BHT) ← Repeat

↓

Homogenize 3 min at 1000 rpm (in homogenizer)

↓

Sonicate 30 sec (in homogenizer) → Sediment

↓

Supernate

↓

Add 2.5 mL 0.88% KCl

↓

Shake vigorously

↓

Centrifuge 10 min at 4,000 rpm (2120 g) → Aspirate, discard aqueous supernate

↓

Aspirate lower, lipid-containing layer and place in tared glass vial

↓

Evaporate solvent with nitrogen (room temperature)

↓

Dry 30 min in vacuum dessicator

↓

Weigh vial with lipid

↓

Add chloroform/methanol (+BHT)

↓

Replace air with nitrogen

↓

Store at -80° C

7

Probe (gefriergetrocknet)

↓

in POTTER-Homogenisiergefäß,
mit Spatel grob zerkleinern

↓

5 ml Chloroform/Methanol (+BHT) hinzufügen ←——

↓ ↑ wieder-holen

3 min mit POTTER bei 1000 U/min homogenisieren

↓ ↑

30 s mit Ultraschall homogenisieren ——→ Sediment
(im Homogenisiergefäß)

↓

Überstand

↓

2.5 ml 0.88% KCl hinzufügen

↓

kräftig schütteln und absetzen lassen

↓

10 min bei 4000 U/min (2120 g) zentrifugieren

↓ ↘

untere Lipid enthaltende Phase absaugen und in vorgewogenes Probengläschen überführen

obere wäßrige Phase absaugen und verwerfen

↓

Lösungsmittel mit Stickstoff verdampfen (Raumtemperatur)

↓

30 min in evakuierten Exsikkator

↓

Probenglas mit Lipid wiegen

↓

Chloroform/Methanol + BHT hinzufügen

↓

Luft durch Stickstoff verdrängen

↓

Aufbewahrung bei -80° C

The specimen is homogenized for about three minutes in a Potter S homogenizer (Braun Co.) with Teflon pestle at 1,000 rpm, after which, in the same container, it is ultrasonicated for 30 sec in an ultrasound homogenizer (Braun Co.). The liquid is then decanted into a centrifuge tube and placed on ice. The homogenate remaining in the homogenizer is again mixed with 5 mL of chloroform/methanol (2/1,v/v) and the process repeated, after which the new material is added to that in the centrifuge tube. The material is cooled in crushed ice during the entire procedure, and stored on ice at the end of the working day.

For extraction, 2.5 mL (one fourth of solvent volume) of 0.88% KCl are added to the centrifuge tube, which is vigorously shaken. After settling, the suspension it is centrifuged 10 min. at 4,000 rpm (2120 g), so that the aqueous phase separates out over the organic phase. Tissue fragments form a dense layer at the phase boundary. The aqueous phase is aspirated (Pasteur pipette) and discarded, while the organic phase, with the extracted lipids is transferred quantitatively to a tared vial. The tissue fragments remain behind, stuck to the centrifuge tube. The solvent is then evaporated with pure nitrogen, and the vial with the extracted lipids stored 30 minutes in a vacuum dessicator, after which it is weighed. Total lipid content is derived by subtracting the vial's tare weight, and correcting for weight changes of the "reference vials", weighed both before and after the lipid vials. The lipids are then dissolvd in chloroform/methanol

(2/1,v/v); air is replaced with nitrogen to prevent oxydation; the lipids are then stored at -80°C. The scheme of the extraction procedure is presented in the Flow Diagram (Fig. 2.7). In all, we we made 497 total lipid analyses, from 42 species and 72 developmental stages.

2.3.3 Analysis of Lipid Classes

The many lipids in an organism belong to a multiplicity of classes (various phospholipids, free fatty acids, triglycerides ["fats"], wax esters, etc...). The usual procedures for quantitative measurements of lipid classes depend on separation by column or thin layer chromatography, followed by gravimetric determinations of each class. These processes, however, require considerable amounts of lipids. One often used method which, however requires major expenditures for equipment, is quantitative analysis of lipid classes by photodensitometry or fluorometry. This metod has the further advantage that, after analysis, the various lipid classes can be recovered and quantitated by methods specific for each class. But this is a time-consuming procedure. Currently, newer procedures, based on "high performance liquid chromatography" (HPLC) are under development. However, we still lack universal HPLC detectors reacting with equal sensitivity to all the various components of a lipid mixture (GURR and JAMES 1980). CHRISTIE 1982) describes the above procedures in detail.

The procedure used here to separate and quantify lipid classes by the IATROSCAN MARK II TH 10 (ACKMAN 1981), was developed at the Institute for Marine Biochemistry at Aberdeen (FRASER et al. 1985). In this method, lipid classes are separated on the principle of Adsorption Chromatography which is also used in Thin Layer Chromatography. In the Iatroscan, however, the stationary phase is not a Thin Layer plate, but a so-called CHROMAROD, a quartz rod coated with sintered kieselguhr [diatomaceous earth] (length, 152 mm; diameter 0.92 mm). Ten rods are attached to a metal frame mounted in the Iatroscan prior to the lipid analysis. A hydrogen (0.75 kg/cm^2)/synthetic air (2,000 mL/min) flame, coupled with a flame ionization detector (FID), is swept (3.1 mm/sec) along the rods and burns away, in a strong electric field, any insoluble residues that might contaminate the rods ("scanning"). When contaminations were not removed by flaming, the Chromarods were cleaned over night in chromate/sulfuric acid (ACKERMAN 1981). The FID registers a current induced by ionized lipid fragments and transmits quantitive signals to an integrator (HP 3392A) connected to the Iatroscan. During a calibration run (no sample) the Iatroscan is zeroed in and the integrator's base-line checked. (19)

Total lipid samples are now applied by microcapillaries (0.5 µL; DESAGA) to the Chromarods, each of which is loaded with 40 µg of lipids in 0.5 µL of chloroform/methanol (2/1). Specimens are always analyzed in duplicate. Following each analysis, the rods are run through the flame a second time, to ensure that no residue of sample had remained. To separate neutral and polar lipids, which

differ in adsorbtion characteristics, two types of solvents were used for chromatography:

Neutral lipids - hexane/diethyl ether/acetic acid 85/15/0.04

Polar lipids - chloroform/methanol/distilled water 70/35/3.5.

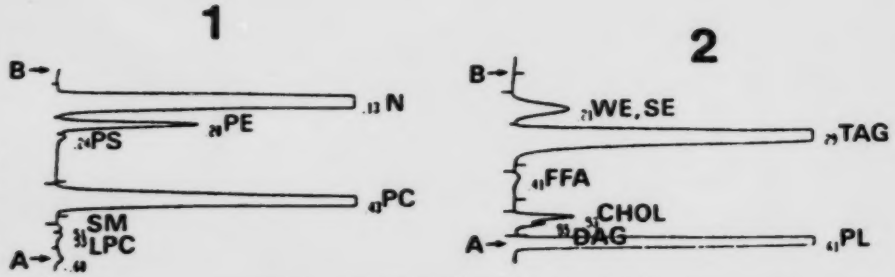
For each separation run, 85 mL of the required solvent were poured into the filter paper-lined developing chamber. One frame with 10 Chromarods (SII) was used for neutral, one for polar lipids. When the solvent front on the rod reaches 10 cm (mark on metal frame), the frame is taken out and placed for 2.5 min in a drying oven at 100° C, to remove the mobile phase (solvent, etc...).

This is followed by Iatroscan analysis, during which the FID signals are fed into the integrator, which produces a graphic representation of the distribution of lipid classes (Fig. 2.8). It is essential for identification of the various lipid classes to know retention time. Quantity of each lipid class is calculated from the areas of the recorded peaks.

Figure 2.8. Separation of Lipids of Euphausia superba

Chromatogram 1: Polar Lipids. Neutral lipid (N); phosphatidylethanolamine (PE); phosphatidylserine (PS); phosphatidylcholine (PC); sphingomyelin (SM); lysophosphatidylcholine (LPC); start (A); solvent front (B).

Chromatogram 2: Neutral Lipids. Wax esters (WE) - sterol esters (SE); triglycerides (TAG); free fatty acids (FFA); cholesterol (CHOL); diglycerides (DAG); polar lipids (PL); start (A); solvent front (B).



Identical quantities of lipids from the different lipid classes give signals of different strengths, so that calibration curves for each lipid class are essential. But as lipids from different classes also interfere with one another, depending on their relative quantitites, FRASER et al. (1985) suggest that the standard lipid mixtures used for calibration resemble in composition the quantitative distribution of lipid classes in the sample to be analyzed. For fish eggs and larvae, rich in phospholipids, they use the following standard mixture: (20)

phosphatidylcholine PC (for phospholipids); triolein TAG (for triglycerides); cholesterol CHOL (for sterols); oleic acid FFA (for free fatty acids); cholesteryl oleate SE (for sterol esters) in the ratios of 15:4:3:2:1.

For zooplankton rich in neutral lipids:

phosphatidylcholine, trioeline, palmityl oleate WE (wax esters) cholesterol, oleic acid as 3:3:3:1:1 (FRASER pers. comm.).

Two additional calibration curves were set up from standard lipid mixtures: for zooplankton with very high triglyceride contents:

TAG, PC, WE, CHOL, FFA as 15:3:3:1.5:1;

for zooplankton rich in wax esters:

TAG, PC, WE, CHOL, FFA as 15:4:3:2:1.

For each standard mixture, dilutions were set so that total lipid contents were 12.5, 25, 50, 75 and 100 mg/mL. All standards were obtained from SIGMA Chemicals Co. Ltd. The same standards were also used to identify the different lipid classes; I also used dioleine and standards for various phospholipids (phosphatidylethanolamine, -serine, -inositol, sphingomyelin, lysophosphatidylcholine).

After a log-log transformation of the calibration data (PARRISCH and ACKMAN 1985) regressions for the different lipid classes from each mixture of standards yielded the equations listed in Table 2.2 (for diolein the triolein equation was used). Testing the coefficient of correlation (r) for significance by the null-hypothesis (one-tailed) resulted in a level of significance of 0.1% (SACHS 1984). The works of KAITARANTA and NICOLAIDES (1981), MURRAY (1985) and of FRASER et al. (1985) show that the behaviours of phosphatidylcholine (PC), phosphatidylethanolamine (PE), phosphatidylserine (PS), phosphatidylinositol (PI), sphingomyelin (SM), and lysophosphatidylcholine (LPC) are sufficiently similar so that the calibration curve for phosphatidylcholine can serve for all the other phospholipids. When comparing the Iatroscan method of analysis with a combination of gravimetric, colourimetric and densitometric procedures, FRASER et al. (1985) did not find significant differences at the 0.5% level of confidence. At the more discriminating 2% level of confidence, there were significant over-estimations of cholesteryl esters and significant under-estimations of phosphatidylethanolamine. For more precise calibrations, therefore, FRASER et al. (1985) suggest adding phosphatidylethanolamine to the mixture of standards. Iatroscan measurement is little affected by degree of saturation, as shown by the comparison between highly unsaturated, and hydrogenated, fish oils (FRASER et al. 1985).

According to FRASER et al. (1985) measures of the various lipid classes are best derived from the ratios between polar and neutral lipids recorded by the chromatography run for polar lipids.

The separation produced by the polar lipid chromatography has the advantage that during the run both polar and neutral lipids migrate with the solvent front from the point of application, so that artifact signals due to application can be distinguished from lipid signals. In chromatographing neutral lipids, the polar lipids remain at the point of application.

[For Table translated below, see following, intercalated page] (21)

Table 2.2 Regression Equations for Calibration Curves

(for each entry, 5 dilutions between 12.5 and 100 mg/mL; 10 readings per dilution level).

[Legend: Lipidklasse = lipid class
Anteil = fraction
Korr.koeff. = coefficient of correlation
%Std.abw. = standard deviation in %

When one adds together all the areas recorded by the integrator for (22) the polar lipid classes, one obtains from the phosphatidylcholine calibration curve a weight that corresponds to the total area. Similarly, one obtains from the area generated by the neutral lipids, and by usinge the calibration curve of neutral lipids, the weight of the neutral lipids corresponding to that area. The percentage distribution of polar and neutral lipids can then be calculated from these two weights. The area of any given polar lipid class, divided by the total area of all polar lipids, and multiplied by the polar lipid fraction of total lipids, yields the percentage fraction of this lipid class in the total lipid sample.

Lipid-klasse	Anteil	$y = a \times^{b}$	Korr.koeff. r	%Std.abw. (min.-max.)
Neutrals:		$y = 3504 \times^{1.8875}$	0.9999	1.5- 8.6
PC:	15	$y = 23741 \times^{1.3806}$	0.9990	2.2- 4.5
TAG:	4	$y = 5767 \times^{1.8432}$	0.9999	4.9-10.4
SE:	1	$y = 9823 \times^{1.4315}$	0.9980	8.8-14.1
FFA:	2	$y = 6297 \times^{1.5680}$	0.9995	8.1-19.1
CHOL:	3	$y = 9412 \times^{1.9490}$	0.9999	6.6-18.2
Neutrals:		$y = 5910 \times^{1.7339}$	0.9961	2.3- 5.9
PC:	3	$y = 23234 \times^{1.3638}$	0.9999	3.3- 6.4
TAG:	3	$y = 8827 \times^{1.7077}$	0.9994	6.1- 8.5
WE:	3	$y = 6876 \times^{1.7367}$	0.9995	6.3-14.3
FFA:	1	$y = 8899 \times^{1.4403}$	0.9977	9.5-34.5
CHOL:	1	$y = 14982 \times^{1.7797}$	0.9991	14.6-18.3
Neutrals:		$y = 10218 \times^{1.5753}$	0.9973	2.8- 6.7
PC:	3	$y = 8403 \times^{1.6599}$	0.9996	5.8- 8.5
TAG:	15	$y = 16817 \times^{1.5158}$	0.9988	4.6- 8.3
WE:	3	$y = 7398 \times^{1.4813}$	0.9997	9.7-17.3
FFA:	1	$y = 7862 \times^{1.3544}$	0.9992	13.6-20.5
CHOL:	1.5	$y = 14311 \times^{1.5910}$	0.9995	10.4-19.4
Neutrals:		$y = 11954 \times^{1.6062}$	0.9956	2.9- 5.4
PC:	4	$y = 11534 \times^{1.5286}$	1.0000	5.0- 7.8
TAG:	3	$y = 12422 \times^{1.4054}$	0.9979	9.4-20.7
WE:	15	$y = 13141 \times^{1.6330}$	0.9987	4.5-11.5
FFA:	1	$y = 8695 \times^{1.3035}$	0.9997	10.3-17.1
CHOL:	2	$y = 14415 \times^{1.6515}$	0.9996	9.4-18.6

Calculations concerning the classes of neutral lipids are somewhat more complex, because their very different behaviours require the use of individual calibration curves for each class. The first step consists in determining the weight of the lipids in the individual classes, using the areas obtained from the chromatogram representing neutral lipids and the relevant calibration curves. Dividing the weight of each class individually by total neutral lipid weight and multiplying by the ratio of neutral lipids to all lipids, one obtains the fraction of that lipid class among all lipids.

Because the calibration curves closely approximate the equations it is permissible to unite all the above calculations into one program. The integrated areas of the individual classes of lipds are fed into a pocket calculator (SHARP PC 1401) and the result is the percentage fraction of each lipid class.

In all, 405 plankton samples were subjected to this lipid class analysis.

3. RESULTS OF ANALYSES (23)

Results of measurements and station data are presented in Tables because the total data are not well amenable to presentation as diagrams. In order to clarify the Tables, the abbreviations used and some other designations, are here briefly explained:

Stat. No.	: trawling station number
Stage	: developmental stage (calyptopis, furcilia, copepodid, female, etc...
Sex	: F = female; M = male
Approx. length	: usually total length; in Euphausiaceae and Mysidaceae distance from anterior margin of eye to end of telson; in fishes = standard length
Total Number (n)	: number of individuals in one sample
Mean WetWt (g)	: average w.w. per individual in g
Mean DryWt (g)	: average d.w. per individual in g
Mean Lipid(g)	: average lipid weight per individual in g
Total Lipid %WetWt	: total lipid as a percentage of wet weight
Total Lipid %DryWt	: total lipid as a percentage of dry weight
Polar	: fraction of polar lipids as percentages of total lipids (lipid content)
Neutral	: fraction of neutral lipids as percentages of total lipids (lipid content)

Abbreviations for individual classes of polar and neutral lipids, each shown as a percentage of lipid content:

Polar Lipids

PE	: phosphatidylethanolamine
PS	: phosphatidylserine
PI	: phosphatidylinositol
PC	: phosphatidylcholine (lecithin)
SM	: sphingomyelin
LPSC	: lysophosphatidylcholine

Neutral Lipids

WE+SE	: wax and steroid ester fraction
TAG	: triglyceride (triacylglycerine)
FFA	: free fatty acids
CHOL	: cholesterol, sterols
DAG	: diglycerides (diacylglycerine)
UNID	: unidentified class of neutral lipids
Mean	: arithmetic mean
Std.Dev.	: standard deviation
0.0	: lipid class not demonstrable, but may be present in minute amounts

In some species the certain lipid classes were combined because chromatographic separation did not sufficiently distinguish the individual groups (PS+PI, SM+LPC, CHOL+DAG).

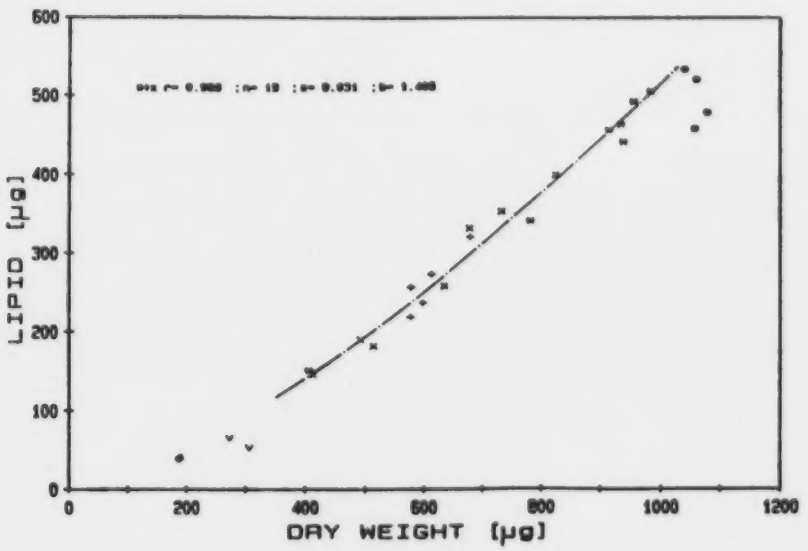
3.1 Copepods

Calanoides acutus (GIESBRECHT 1902)

Copepodid C V instars and females of Calanoides acutus from November 1983 (Antarctic Peninsula) and January/February 1985 (Weddell Sea) were examined. As is shown in Table 3.1. and Figures 3.1 to 3.4, there are distinct differences between these two seasons and/or locations. The C V stages from November, with 20.7% lipids, contain, on a percentage basis, less than half the average lipids of the C V stages of January/February 1985 from the Weddell Sea (44.1%). The total amount of lipids in the November copepodids of the Peninsula is smaller by about one order of magnitude than that of C V stages from the Vestkapp Box, though in percent this difference becomes less important because of differences in body weights. Similar differences are noted among females. In November 1983, off the Antarctic Peninsula these have a mean lipid content of 20.6%, but in the Weddell Sea (January Vestakapp Box) the content averages 46.9%. Here too, the large differences in absolute values are remarkable, as the Weddell Sea animals weigh three to four times more, and contain approximately eight times more lipids by weight. What is remarkable is the low body weight at which Antarctic Peninsula C. acutus can produce, by November, C V stages and females (Tab. 3.1 and Fig. 3.1). (24)

There are also clear differences in body and lipid weights apparent when one compares the data from the January Vestkapp Box with those from the Filchner Depression region and the February Vestkapp Box. In the latter two regions, the C V stages are, on average, one fourth lighter and one third "leaner". It is possible that the lighter copepodids represent a younger C V stage whereas the C V stages of the January Vestkapp Box -- with one exception -- are more advanced and have already nearly reached the weight of females in this Box. Figure 3.1 shows the absolute increase in lipids as a function of dry weight.

Figure 3.1. Lipid to Dry Weights relation in Calanoides acutus (Nov. 1983, Antaractic Peninsula: CV #, females v; Jan./Feb. 1985, Weddell Sea: C V * (Jan. Box), C V + (Vahsel Bay/Gould Bay), C V x (Feb. Box) Females • (Jan. Box); log-log regression.



In spite of geographical and chronological differences in sampling, the C V data give a uniform regression line without great deviations. The variability in weight of the C V stages -- 200 animals each -- within a Box are clearly apparent. The few data relating to females of the January Vestkapp Box suggest that reproductive processes have caused changes in lipid metabolism.

Table 3.1. Station and Measurement Data of Calanoides acutus copepodid V (C5), Females (F); Antarctic Peninsula 1983; Weddell Sea 1985. (25)

[See over]

(page 36a)

Tab. 3.1. Stationsdaten und Messergebnisse von Calanoides acutus Copepodit 5 (C5), Females (F); Antarktische Halbinsel 1983; Weddell See 1985

Stat. No.	Date D/M/Y	Haul Depth (m)	Stage C5,F	Total Number (n)	Mean WetWt (g)	Mean DryWt (g)	Mean Lipid (g)	Total Lipid %WetWt	Total Lipid %DryWt	Lipid Class Composition in Percent of Total Lipid: Polar	Neutral	PE	PS+ PI	PC	SM	LPC	WE+ SE	TAG	FFA	CHOL	DAG
143	04/11/83	200-0	C5	100	0.00177	0.000188	0.000039	2.2	20.7	22.9	77.1	5.4	0.6	14.3	2.1	0.5	63.5	3.6	6.9	2.0	1.0
306	07/02/85	215-0	C5	200	0.00408	0.000577	0.000219	5.4	38.0												
299	05/02/85	240-0	C5	200	0.00380	0.000578	0.000257	6.8	44.5	5.0	95.0	1.8	0.0	2.8	0.3	0.1	92.0	2.4	0.0	0.7	0.0
298	05/02/85	198-0	C5	100	0.00425	0.000598	0.000237	5.6	39.6												
307	08/02/85	230-0	C5	200	0.00406	0.000613	0.000273	6.7	44.6	4.1	95.9	1.2	0.0	2.7	0.2	0.0	92.9	3.0	0.0	0.0	0.0
309	09/02/85	220-0	C5	200	0.00401	0.000680	0.000320	8.0	47.1	3.9	96.1	1.1	0.0	2.6	0.2	0.0	92.9	3.1	0.0	0.0	0.0
Mean					0.00404	0.000609	0.000261	6.5	42.7	4.3	95.7	1.4	0.0	2.7	0.2	0.0	92.6	2.8	0.0	0.2	0.0
317	12/02/85	175-0	C5	200	0.00382	0.000413	0.000146	3.8	35.3	7.6	92.4	2.4	0.0	4.7	0.5	0.0	88.4	3.1	0.0	0.9	0.0
336	16/02/85	180-0	C5	200	0.00387	0.000492	0.000190	4.9	38.7	5.4	94.6	1.6	0.0	3.5	0.0	0.4	90.9	3.2	0.0	0.4	0.0
315	12/02/85	190-0	C5	200	0.00405	0.000514	0.000182	4.5	35.5												
318	12/02/85	205-0	C5	100	0.00395	0.000635	0.000258	6.5	40.6												
349	21/02/85	165-0	C5	50	0.00389	0.000679	0.000331	8.5	48.8	3.8	96.2	1.6	0.0	1.9	0.0	0.3	93.3	2.9	0.0	0.0	0.0
320	13/02/85	220-0	C5	200	0.00406	0.000734	0.000352	8.7	48.0	3.3	96.7	1.3	0.0	1.8	0.0	0.1	93.8	2.9	0.0	0.0	0.0
327	14/02/85	205-0	C5	200	0.00391	0.000825	0.000398	10.2	48.3	2.3	97.7	1.0	0.0	1.4	0.0	0.0	94.6	3.0	0.0	0.0	0.0
Mean					0.00393	0.000613	0.000265	6.7	42.1	4.5	95.5	1.6	0.0	2.7	0.1	0.2	92.2	3.0	0.0	0.3	0.0
252	23/01/85	210-0	C5	196	0.00334	0.000406	0.000151	4.5	37.1	5.8	94.2	1.8	0.0	3.2	0.4	0.4	90.1	2.7	0.6	0.9	0.0
254	23/01/85	215-0	C5	200	0.00407	0.000783	0.000340	8.4	43.4												
263	25/01/85	200-0	C5	200	0.00470	0.000915	0.000455	9.7	49.7												
258	24/01/85	227-0	C5	200	0.00473	0.000935	0.000462	9.8	49.4	2.8	97.2	1.0	0.2	1.4	0.0	0.2	93.7	3.5	0.0	0.0	0.0
271	27/01/85	190-0	C5	200	0.00458	0.000939	0.000440	9.6	46.9												
267	26/01/85	202-0	C5	200	0.00464	0.000956	0.000491	10.6	51.3												
267	26/01/85	202-0	C5	200	0.00483	0.000984	0.000504	10.4	51.2	2.6	97.4	1.0	0.0	1.5	0.1	0.0	93.8	3.6	0.0	0.0	0.0
Mean					0.00441	0.000845	0.000406	9.0	47.0	3.7	96.3	1.3	0.1	2.0	0.2	0.2	92.5	3.3	0.2	0.3	0.0
143	04/11/83	200-0	F	100	0.00186	0.000273	0.000065	3.5	23.8	21.1	78.9	5.2	0.6	12.1	2.6	0.6	66.5	4.1	5.8	1.5	1.0
143	04/11/83	200-0	F	100	0.00264	0.000306	0.000053	2.0	17.3	19.4	80.6	4.9	0.1	13.0	0.9	0.5	69.3	3.0	5.1	1.7	1.5
Mean					0.00225	0.000290	0.000059	2.8	20.6	20.2	79.7	5.1	0.4	12.6	1.8	0.6	67.9	3.6	5.5	1.6	1.3
258	24/01/85	227-0	F	58	0.00600	0.001041	0.000532	8.9	51.1	3.8	96.2	1.1	0.0	2.3	0.0	0.4	91.9	4.0	0.0	0.4	0.0
263	25/01/85	200-0	F	100	0.00633	0.001058	0.000457	7.2	43.2												
267	26/01/85	202-0	F	150	0.00604	0.001061	0.000519	8.6	48.9	3.4	96.6	1.1	0.0	2.2	0.1	0.0	92.2	4.5	0.0	0.0	0.0
271	27/01/85	190-0	F	200	0.00615	0.001079	0.000477	7.8	44.2												
Mean					0.00613	0.001059	0.000496	8.1	46.9	3.6	96.4	1.1	0.0	2.3	0.1	0.2	92.0	4.3	0.0	0.2	0.0

Figure 3.2. Lipid content of Calanoides acutus during the Period of Study (C V stages x; females •) (26)

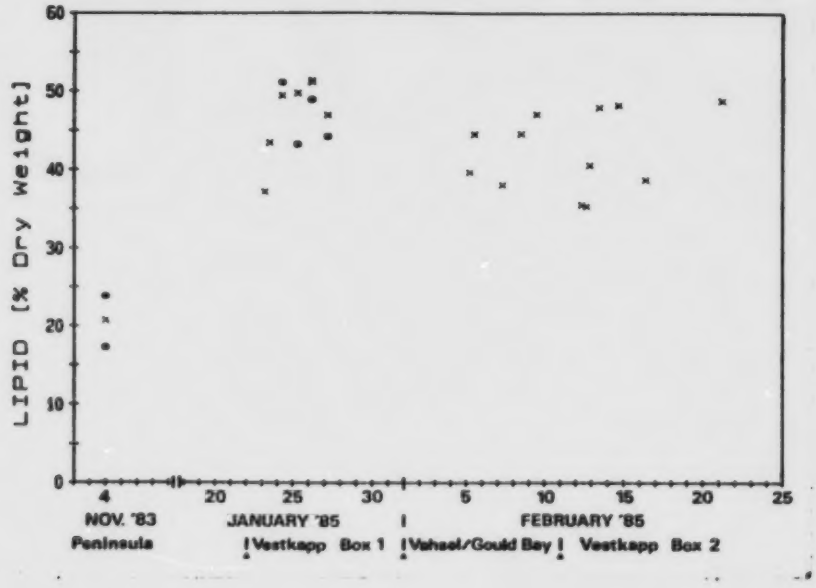


Figure 3.3. Lipid Classes (% d. w.)/Lipid Content in Calanoides acutus (Antarctic Peninsula, Weddell Sea); wax esters *; phosphatidylcholine o; phosphatidylethanolamine +; linear regression.

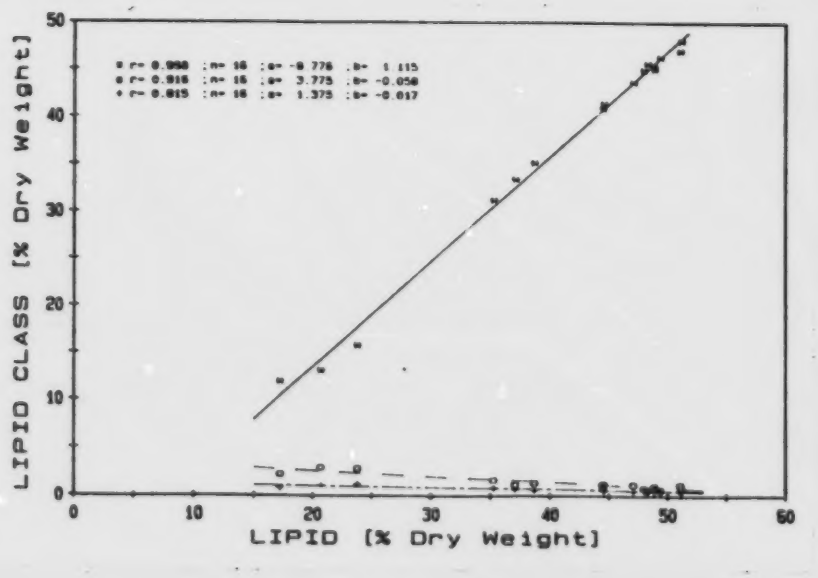
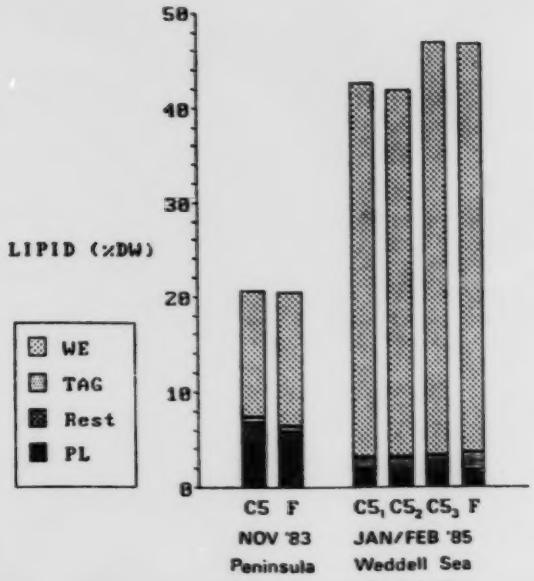


Figure 3.2 represents lipid content (as % d.w.) in C. acutus as a function of the time of study. There are no significant differences in terms of lipid accumulation between the several groups of C V caught in the Weddell Sea at various times ($r = 0.28$). As early as the end of January the animals examined contained a maximum of 51% lipids; mean lipid content in the January Vestkapp Box was 47.0%, then declined to approximately 42-43% in the area of the Filchner Depression (Vahsel Bay/Gould Bay) and, later, in the February-Vestkapp Box. However, if one assumes that in C. acutus it is primarily individual level of development rather than seasonal factors which determines lipd content during the season (feeding phase), as Fig. 3.1 suggests -- i.e. that less heavy animals have lower lipid contents -- it would explain the lower total lipid levels in less ponderous animals caught later in the area of the Filchner Depression and the February Vestkapp Box. The regression line in Fig. 3.1 can be used as a "calibration curve". As the relationship between lipid weight and dry weight is that of a power function with $b = 1.4$, the percentage increase of lipids in the C V stages, with increasing dry weight, from 35% in the lightest C V stages, to 50% by the end of growth, and transition to mature female.

Figure 3.3 demonstrates that lipid accumulation is due nearly exclusively to increases in wax esters, while the fraction of phospholipids, phosphatidylcholine and -ethanolamine, decreases slightly. Figure 3.4 shows changes in lipid classes between animals from November (Antarctic Peninsula) and January/February (Weddell Sea). The phospholipids of C V stages and of females from November 1983, with

respective lipid content fractions of 22.9% and 20.2%; wax ester fractions are 63.5% and 67.9%. On the other hand, the phospholipid fraction of the C V and females from the Weddell Sea is extremely low, at 4%, while wax esters make up 92% of total lipids.

Figure 3.4. Lipid Content and Composition in Calanoides acutus. ($C5_1$: C V [Vahsel Bay/Gould Bay]; $C5_2$: C V [Feb. Box]; $C5_3$: C V [Jan.-Box] in order of d. w.; F = females (Antarctic Peninsula or Jan. Box])



Calanus propinquus BRADY 1883 (28)

For this species, only Weddell Sea specimens were available, but in addition to C V stages and females, younger copepodids (C II, C III) and males were represented (Tab. 3.2 and Figs. 3.5 to 3.8). Among copepodids, the C II instars (February Vestkapp Box) contained the least amount of lipids (18.1%), primarily triglycerides (42.3%), wax esters (26.8%) and phospholipids (24%). Lipid content increases to 20.7% in C III (February Vestkapp Box) while the relative amount of triglycerides (68.5%) increases at the expense of wax esters (10.6%) and phospholipids (16.0%) (Fig. 3.5).

The C V stages from the two Boxes are distinctly different (Figs. 3.5 to 3.8). During the January Vestkapp Box their lipid content is 25.6%; percentages of phospholipids (7.5%) and wax esters (4.1%) are decreased compared to those of the C III stage (February Box); triglycerides make up the major fraction (84.7%). This evolution continues throughout the February Box: the lipid contents of C V approximately doubles (47.1%), most of it (93.8%) as triglycerides. The C V sample of this species designated by (R) in Table 3.2 was exceptional because of a red colouration of the posterior half of the cephalothoraces, but the lipids were similar to those of the other animals.

The situation of the C. propinquus females resembles that of the C V stage (Figs. 3.5, 3.6, 3.8). During the January-Vestkapp Box their lipid content is 25.3%, and triglycerides (83.3%) predominate.

During the February-Box, the lipid content of females increases to an average of 42.8%, primarily triglycerides (92.8%). Those females in which half the cephalothorax was red (R), and which were studied separately, clearly are different from other females (body weight, lipid and triglyceride contents all lower). The comparatively rare males were caught during the February Box. Body weight and lipid content (24,3%) are distinctly lower than in females; triglycerides only constitute 71.5% of the lipids (wax esters 14.5%, phospholipids 12.6%; Fig. 3.5).

Overall, therefore, the C V stages and females of this herbivorous copepod species show a marked increase in lipids, as triglycerides, during the course of three to four weeks. One should, however, not forget that the animals collected during the February Box belong to a different population than those of the January Box, which have since drifted away on the current.

Figure 3.7 represents the weigths of the various lipid classes in C. propinquus as a function of dry weight. The curve describes the increase in triglycerides of copepodids of the February Box with increasing dry weight. A seond curve details this correlation for females from the February Box, in which the triglyceride/dry weight ratio is lower (cause: ? reproduction). Data from C V stages and females of the January Box do not fit regressions of the February Box. The triglyceride/dry weight ratio is always lower. Phospholipids (PC, PE) increased only minimally. Figure 3.7 shows these differences to be caused nearly exclusively by triglyceride storage.

The behaviours of the various lipid classes (TAG, PC, PE), as a function of the lipid content, is detailed in Figure 3.8, which clearly shows the major, and linear, increase in triglycerides, while phospholipids hardly change.

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[For Table and Figures translated below, see following intercalated pages]

Table 3.2. Station and Measurement Data for Calanus propinquus, copepodites C II (C2), C III (C3), C V (C5), females (F), males (M), pigmented variant (R). Weddell Sea 1985 (29)

Figure 3.5 Lipid Content and Composition in Calanus propinquus (C II = C2, C III = C3, C V = C5, F = female, M = male) (30)

Figure 3.6 Lipid Content of Calanus propinquus During Study Period (C II +, C III *, C V x, ·—·—· ; females ●— — —; males o; linear regression

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Figure 3.7 Lipid Class Weight/Dry Weight of Calanus propinquus (Triglycerides: Jan. Box: *, Feb Box: C II, C III, C V x, females ●; phosphatidylcholine o; phosphatidylethanolamine +) (31)

Figure 3.8 Lipid Classes (% d.w.)/Lipid Content in Calanus propinquus (Triglycerides: Jan. Box x, Feb. Box *, phosphatidylcholine o, phosphatidylethanolamine +)

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Rhincalanus gigas BRADY 1883 (32)

Results for Rhincalanus gigas are given in Table 3.3 and Figures 3.9 to 3.11. Animals caught in November 1983 off the Antarctic Peninsula are quite different from those of the Weddell Sea in January/February 1985. Compared to the latter, the three Antarctic Peninsula stages examined (C IV, C V, females) weigh less (C V, females), have lower

Tab. 3.8. Stationsdaten und Messergebnisse von Calanus propinquus Copepodite C2, C3, C5, Females (F), Males (M), Farbvariante (R); Weddell See 1985

Stat. No.	Date D/M/Y	Haul Depth (m)	Stage C,F,M	Total Number (n)	Mean WetWt (g)	Mean DryWt (g)	Mean Lipid (g)	Total Lipid %WetWt	Total Lipid %DryWt	Lipid Class Composition in Percent of Total Lipid: Polar	Neutral	PE	PS+PI	PC	SM	LPC	WE+SE	TAG	FFA	CHOL	DAG
326	14/02/85	225-0	C2	175	0.00064	0.000079	0.000014	2.2	18.1	24.0	76.0	10.7	0.3	11.9	0.7	0.3	26.8	42.3	4.0	3.0	0.0
318	12/02/85	205-0	C3	170	0.00173	0.000218	0.000040	2.3	18.2	16.3	83.7	7.4	0.3	7.5	0.8	0.3	10.0	68.5	2.7	2.5	0.0
324	14/02/85	205-0	C3	92	0.00211	0.000254	0.000059	2.8	23.4	14.8	85.1	4.9	0.3	9.1	0.5	0.0	10.7	70.1	2.3	1.9	0.0
326	14/02/85	225-0	C3	115	0.00185	0.000259	0.000053	2.9	20.6	16.9	83.1	7.9	0.5	7.7	0.8	0.0	11.0	67.0	2.8	2.3	0.0
Mean					0.00190	0.000244	0.000051	2.7	20.7	16.0	84.0	6.7	0.4	8.1	0.7	0.1	10.6	68.5	2.6	2.2	0.0
254	23/01/85	215-0	C5	45	0.00584	0.000763	0.000216	3.7	28.3	7.9	92.1	3.2	0.3	3.9	0.4	0.1	5.8	82.7	2.4	1.1	0.0
259	24/01/85	220-0	C5	200	0.00950	0.000950	0.000210	2.2	22.1	7.1	92.9	2.9	0.1	3.4	0.2	0.5	2.7	85.3	2.9	1.9	0.0
260	24/01/85	190-0	C5	117	0.01038	0.001045	0.000278	2.7	26.6	7.2	92.8	2.9	0.0	3.7	0.2	0.4	4.1	86.1	1.4	1.2	0.0
264	26/01/85	220-0	C5	100	0.01008	0.001031	0.000261	2.6	25.3	7.6	92.4	2.8	0.0	3.5	0.4	0.9	3.6	84.7	2.6	1.5	0.0
Mean					0.00895	0.000947	0.000241	2.8	25.6	7.5	92.5	3.0	0.1	3.6	0.3	0.5	4.1	84.7	2.3	1.4	0.0
318	12/02/85	205-0	C5	200	0.00546	0.001096	0.000449	8.2	41.0	4.7	95.3	1.6	0.0	2.4	0.3	0.4	1.2	93.4	0.0	0.6	0.0
324	14/02/85	205-0	C5	135	0.00542	0.001327	0.000648	11.9	48.8	5.0	95.0	2.0	0.0	2.6	0.1	0.2	1.5	92.8	0.0	0.8	0.0
326	14/02/85	225-0	C5	200	0.00530	0.001263	0.000552	10.4	43.7	3.9	96.1	1.4	0.0	2.0	0.1	0.4	1.2	94.4	0.0	0.5	0.0
339	16/02/85	205-0	C5(R)	168	0.00606	0.001250	0.000603	9.9	48.2	4.5	95.5	1.7	0.0	2.3	0.1	0.3	1.5	93.5	0.0	0.5	0.0
339	16/02/85	205-0	C5	200	0.00562	0.001307	0.000591	10.5	45.2	4.7	95.2	1.7	0.0	2.2	0.3	0.5	0.5	93.8	0.0	1.0	0.0
349	21/02/85	165-0	C5	81	0.00618	0.001543	0.000859	13.9	55.7	3.9	96.1	1.6	0.0	2.1	0.2	0.0	0.7	95.0	0.0	0.4	0.0
Mean					0.00567	0.001298	0.000617	10.8	47.1	4.5	95.5	1.7	0.0	2.3	0.2	0.3	1.1	93.8	0.0	0.6	0.0
254	23/01/85	215-0	F	46	0.00929	0.001618	0.000433	4.7	30.6	7.4	92.6	2.2	0.0	4.2	0.4	0.6	6.6	82.1	2.4	1.4	0.0
259	24/01/85	220-0	F	200	0.01145	0.001544	0.000408	3.6	26.4	6.9	93.1	2.3	0.0	4.0	0.2	0.3	1.7*	87.9	2.1	1.4	0.0
260	24/01/85	190-0	F	200	0.01494	0.001736	0.000474	3.2	27.3	6.9	93.1	2.3	0.0	4.2	0.3	0.0	2.3	89.7	0.0	1.1	0.0
262	25/01/85	215-0	F	200	0.01482	0.001634	0.000263	1.8	16.1	19.2	80.8	5.5	0.1	12.5	1.0	0.0	3.1	72.6	2.6	2.5	0.0
264	26/01/85	220-0	F	200	0.01190	0.001655	0.000428	3.6	25.9	9.3	90.7	3.5	0.0	4.9	0.7	0.2	1.4	84.3	2.8	1.7	0.6
Mean					0.01248	0.001597	0.000401	3.4	25.3	9.9	90.1	3.2	0.0	6.0	0.5	0.2	3.0	83.3	2.0	1.6	0.1
318	12/02/85	205-0	F	200	0.00764	0.001560	0.000589	7.7	37.8	4.2	95.8	1.0	0.0	2.3	0.2	0.7	1.2	92.6	0.9	1.1	0.0
324	14/02/85	205-0	F	127	0.00775	0.001877	0.000888	11.5	47.3	4.4	95.6	1.6	0.0	2.6	0.2	0.0	1.5	93.5	0.0	0.7	0.0
326	14/02/85	225-0	F	240	0.00777	0.001695	0.000667	8.6	39.4	4.1	95.9	1.4	0.0	2.4	0.3	0.0	1.2	94.3	0.0	0.4	0.0
339	16/02/85	205-0	F(R)	21	0.00760	0.001428	0.000500	6.6	35.0	7.0	93.0	2.6	0.1	3.7	0.7	0.0	6.1	86.0	0.0	0.9	0.0
339	16/02/85	205-0	F	200	0.00854	0.001894	0.000807	9.5	42.6	4.4	95.6	1.7	0.0	2.4	0.3	0.0	1.2	94.1	0.0	0.3	0.0
349	21/02/85	165-0	F	160	0.00754	0.002168	0.001189	15.8	54.8	3.4	96.6	1.4	0.0	1.8	0.1	0.0	0.0	96.6	0.0	0.0	0.0
Mean					0.00780	0.001770	0.000773	9.9	42.8	4.6	95.4	1.6	0.0	2.5	0.3	0.1	1.9	92.8	0.2	0.6	0.0
339	16/02/85	205-0	M(R)	12	0.00676	0.001020	0.000248	3.7	24.3	12.6	87.4	4.3	0.2	6.8	1.3	0.0	14.5	71.5	0.0	1.3	0.0

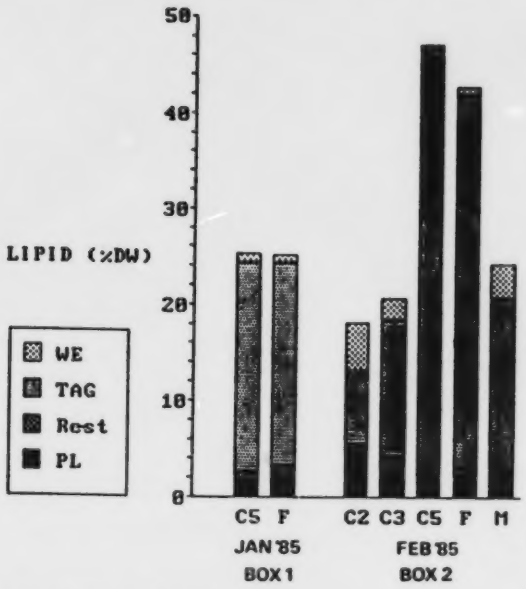


Abb. 3.5. Lipidgehalt und Lipidzusammensetzung von *Calanus propinquus* (C2, C3, C5: C2-, C3-, C5-Stadium, F: Weibchen, M: Männchen)

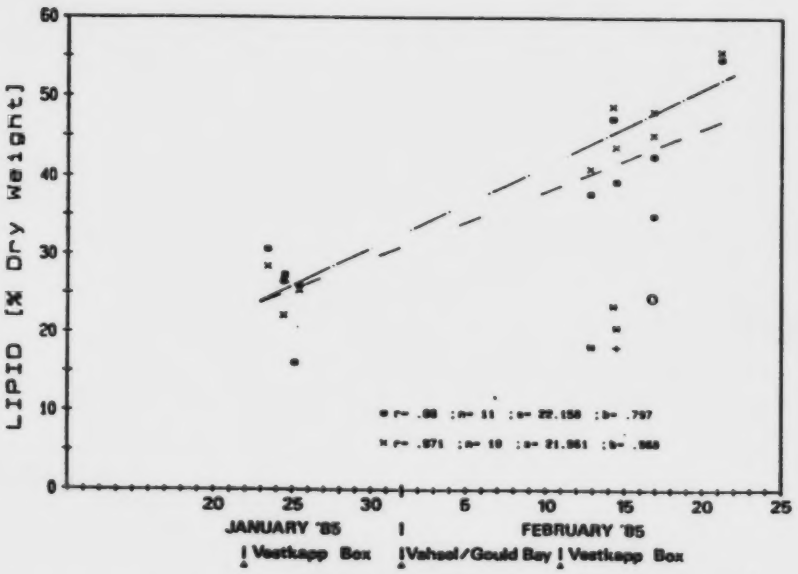


Abb. 3.6. Lipidgehalt von *Calanus propinquus* im Verlaufe des Untersuchungszeitraums (C2 +, C3 *, C5 x _____·_____ ; Weibchen • ___ ___ ___ ; Männchen o; lineare Regression)

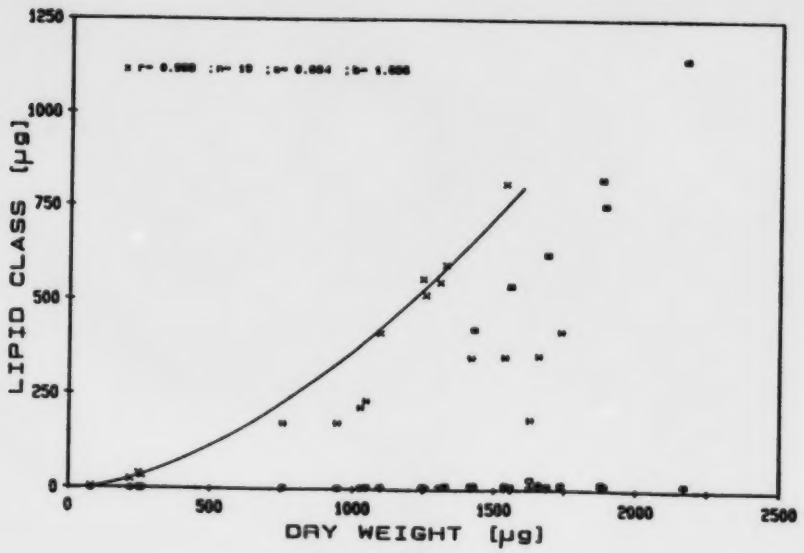


Abb. 3.7. Lipidklassengewicht/Trockengewicht von *Calanus propinquus* (Triglycerid: Jan.-Box: ⁎, Feb.-Box: C2, C3, C5 x, Weibchen ●; Phosphatidylcholin o; Phosphatidylethanolamin +)

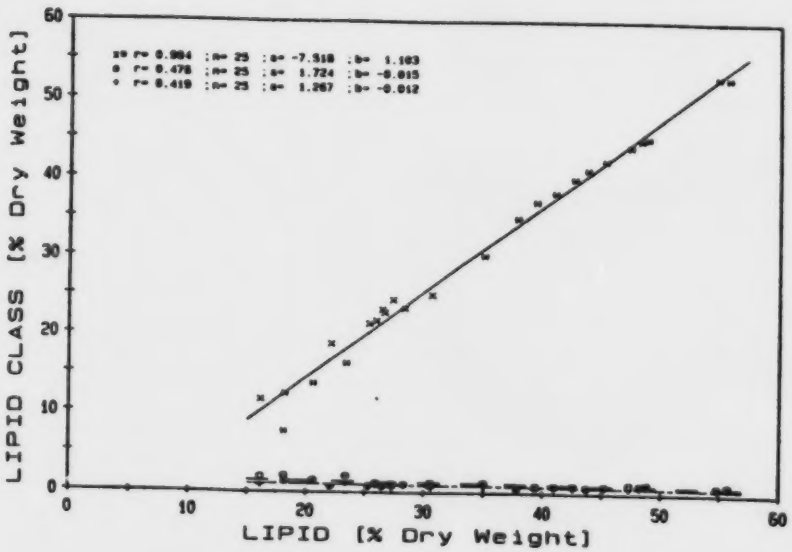


Abb. 3.8. Lipidklassen (% TG)/Lipidgehalt von *Calanus propinquus* (Triglycerid: Jan.-Box: x, Feb.-Box: ⁎; Phosphatidylcholin o; Phosphatidylethanolamin +)

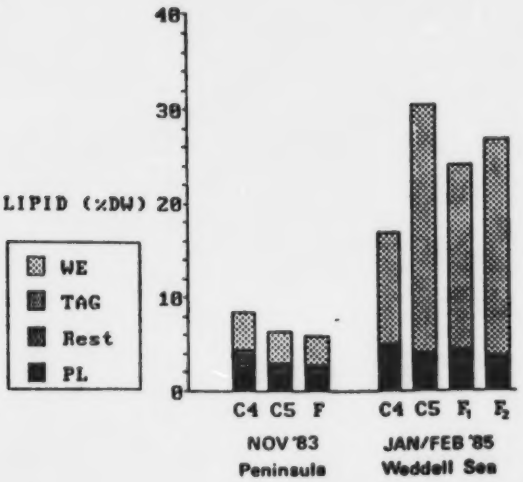
lipid contents (6.0-8.6%), larger phospholipid (28.2%-29.3%), and smaller wax ester (49.2%-54.8%) fractions.

R. gigas C III collected in the Weddell Sea did not contain sufficient lipids for proper analysis, which is why the relevant data are missing from Table 3.3. However, a lipid class analysis of the C III was possible. The majority of the C III lipds are wax esters (61.8%), triglycerides (15.2%) and phospholipids (19.5%). Lipid content of C IV from the Weddell Sea are 17.1%; wax esters (69.5%) have increased slightly over the C III satge, while triglycerides (9.6%) and phospholipids (17.2%) have decreased slightly (Fig. 3.9). This change carries over to C V. The clear increase of lipid content (30.7%) correlates with a further increase in the wax ester fraction (86.7%). There were no significant differences in lipid development between the Boxes. The coefficient of regression ($r = 0.52$) proves that the minor, time-related, decrease in lipids in C V is not significant. In the females, average lipid content rises slightly over three to four weeks (Jan. Box, Feb. Box) from 24.2% to 27.0%, while the wax ester fraction simultaneously increases slightly from 82.3% to 86.2% (Fig. 3.9). These trends, as well, are not significant.

Figure 3.10 shows the absolute lipid increase as a function of rising dry weight. There are no clear differences between samples from the two Vestkapp Boxes (January, February). Lipid weight of the C IV and C V copepodids grows as a power function, whereas the curve representing the females is displaced (lower lipid/dry weight ratio;

cause ? reproduction). Animals caught off the Antarctic Peninsula in November 1983 had very low lipid and dry weights (Fig. 3.10).

Figure 3.9. Lipid Contents and Composition in Rhincalanus gigas (F-1: females (Jan. Box), F-2 females (Feb. Box)



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[For Table and Figures translated below see following intercalated pages]

Table 3.3. Station and Measurement Data for Rhincalanus gigas copepodids C III, C IV, C V, females (F); Antarctic Peninsula 1983, Weddell Sea 1985 (33)

Figure 3.10. Lipid Weight/Dry Weight Ratios in Rhincalanus gigas (Nov. 1983, Antarctic Peninsula: C IV +, C V v, females #; Jan./Feb. 1985 Weddell Sea: C IV *, C V x, females ●, log-log regression (34)

Figure 3.11. Lipid Classes (% d.w.)/Lipid Content in Rhincalanus gigas (Antarctic Peninsula, Weddell Sea); wax esters *; phosphatidylcholine o; phosphatidylethanolamine +; linear regression

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Tab. 3.3. Stationsdaten und Messergebnisse von Rhincalanus gigas Copepodite C3, C4, C5, Females (F); Antarktische Halbinsel 1983, Weddell See 1985

Stat. No.	Date D/M/Y	Haul Depth (m)	Stage C, F	Total Number (n)	Mean WetWt (g)	Mean DryWt (g)	Mean Lipid (g)	Total Lipid %WetWt	Total Lipid %DryWt	Lipid Class Composition in Percent of Total Lipid: Polar	Neutral	PE	PS+PI	PC	SM	LPC	WE+SE	TAG	FFA	CHOL	DAG
327	14/02/85	205-0	C3	40	0.0020	0.00014				19.5	80.5	6.7	0.4	11.7	0.2	0.6	61.8	15.2	0.0	3.5	0.0
143	04/11/83	200-0	C4	55	0.0049	0.00034	0.00003	0.6	8.6	28.9	71.1	8.6	0.8	16.2	1.6	1.7	49.2	5.0	9.2	3.4	4.3
327	14/02/85	205-0	C4	62	0.0049	0.00033	0.00006	1.2	18.1	16.3	83.7	6.4	0.5	9.0	0.1	0.3	68.7	12.6	0.0	2.4	0.0
349	21/02/85	165-0	C4	59	0.0055	0.00032	0.00005	1.0	16.2	18.2	81.8	6.0	0.3	11.2	0.2	0.5	70.4	6.5	2.0	3.0	0.0
Mean					0.0052	0.00033	0.00006	1.1	17.1	17.2	82.7	6.2	0.4	10.1	0.2	0.4	69.5	9.6	1.0	2.7	0.0
143	04/11/83	200-0	C5	50	0.0068	0.00055	0.00004	0.5	6.5	28.2	71.8	6.6	1.0	17.1	1.3	2.2	53.9	6.1	4.5	2.7	4.7
267	26/01/85	202-0	C5	43	0.0138	0.00123	0.00038	2.7	30.7	6.8	93.2	2.4	0.0	3.8	0.0	0.7	86.4	5.7	0.0	1.1	0.0
271	27/01/85	190-0	C5	34	0.0110	0.00107	0.00035	3.2	32.5	6.2	93.8	1.9	0.1	3.9	0.0	0.3	86.5	6.2	0.0	1.1	0.0
320	13/02/85	220-0	C5	50	0.0120	0.00120	0.00039	3.3	32.6	5.6	94.4	2.0	0.0	3.3	0.0	0.3	88.0	5.5	0.0	0.9	0.0
327	14/02/85	205-0	C5	41	0.0122	0.00124	0.00039	3.2	31.7	5.3	94.7	1.9	0.1	3.0	0.0	0.3	88.6	5.0	0.0	1.0	0.0
349	21/02/85	165-0	C5	19	0.0113	0.00085	0.00022	1.9	25.8	8.7	91.3	2.7	0.3	5.2	0.1	0.4	84.0	5.6	0.0	1.7	0.0
Mean					0.0120	0.00112	0.00035	2.9	30.7	6.5	93.5	2.2	0.1	3.8	0.0	0.4	86.7	5.6	0.0	1.2	0.0
143	04/11/83	200-0	F	50	0.0089	0.00066	0.00003	0.3	4.6	32.9	67.1	7.5	2.3	18.9	1.7	2.6	48.1	4.8	6.1	3.0	5.0
143	04/11/83	200-0	F	49	0.0109	0.00072	0.00005	0.5	7.4	25.8	74.2	7.7	1.0	15.4	0.7	1.0	61.5	1.9	5.0	3.9	1.9
Mean					0.0099	0.00069	0.00004	0.4	6.0	29.3	70.6	7.6	1.7	17.2	1.2	1.8	54.8	3.4	5.6	3.5	3.5
254	23/01/85	215-0	F	27	0.0181	0.00138	0.00029	1.6	21.3	12.1	87.9	4.4	0.3	6.7	0.1	0.6	79.7	4.7	1.3	2.2	0.0
267	26/01/85	202-0	F	125	0.0207	0.00189	0.00047	2.3	24.8	7.4	92.6	2.2	0.1	4.6	0.1	0.5	84.9	6.4	0.0	1.2	0.0
271	27/01/85	190-0	F	92	0.0177	0.00170	0.00045	2.6	26.5												
Mean					0.0188	0.00166	0.00041	2.2	24.2	9.8	90.2	3.3	0.2	5.7	0.1	0.6	82.3	5.6	0.7	1.7	0.0
320	13/02/85	220-0	F	73	0.0183	0.00186	0.00051	2.8	27.6	7.2	92.8	2.7	0.1	4.1	0.0	0.3	86.1	5.4	0.0	1.3	0.0
327	14/02/85	205-0	F	45	0.0181	0.00174	0.00043	2.4	24.6												
349	21/02/85	165-0	F	10	0.0191	0.00175	0.00051	2.6	28.8	7.9	92.1	3.0	0.2	4.3	0.0	0.3	86.2	4.4	0.0	1.6	0.0
Mean					0.0185	0.00178	0.00048	2.6	27.0	7.6	92.4	2.9	0.2	4.2	0.0	0.3	86.1	4.9	0.0	1.5	0.0

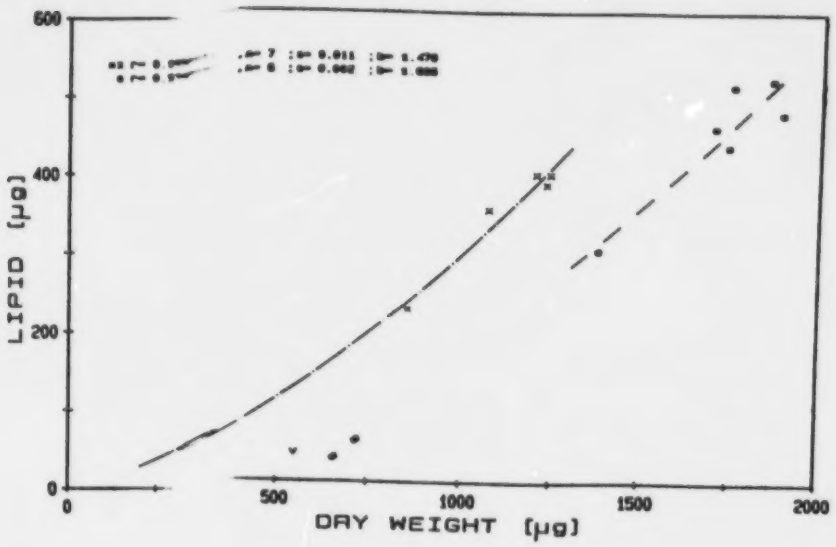

Abb. 3.10. Lipid- / Trockengewichtsbeziehung von *Rhincalanus gigas* (Nov. 1983, Antarktische Halbinsel: C4 +, C5 v, Weibchen *; Jan./Feb. 1985, Weddellmeer: C4 x, C5 x, Weibchen •, doppelt logarithmische Regression)

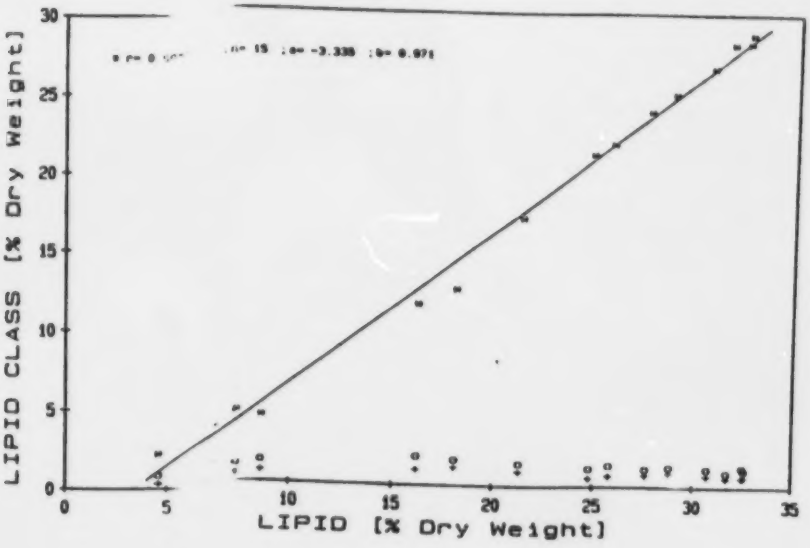

Abb. 3.11. Lipidklassen (% TG)/Lipidgehalt von *Rhincalanus gigas* (Antarktische Halbinsel, Weddellmeer); Wachsester *; Phosphatidylcholin o; Phosphatidylethanolamin +; lineare Regression

Figure 3.11 describes the interrelation between the various lipid classes (WE, PC, PE) and the lipid fraction of dry weight. There are only small changes in the phospholipids, but a significant linear relationship between wax ester and total lipid increases, both in terms of absolute amounts (not shown) and of dry weight (Fig. 3.11). Data for the animals from the Antarctic Peninsula (Nov. 1983) fit the same curve as those from the Weddell Sea. (35)

Metridia gerlachei GIESBRECHT 1902

All of the data for Metridia gerlachei shown in Table 3.4 and Figures 3.12 and 3.13 come from specimens collected in the southern Weddell Sea (January and February Vestkapp Box, Filchner Depression) C IV material was sufficient only for determination of lipid classes, the major fraction of which are wax esters (39.9%), triglycerides (23.9%) and phospholipids (18.8%). This distribution is nearly the same as that in the few C V analyzed, except that there are slightly more phospholipids here. C V lipid contents in the January Box were 20.4%, in the February Box 22.3%. The individual lipid class fractions in the two Boxes vary hardly from one another, except that the phospholipid fraction is slightly higher in the February Box (Fig. 3.12).

The changes seen in the large number of females of M. gerlachei are interesting. Lipid contents in the January Vestkapp box averaged 15.6%. This increases in the region of the Filchner Depression to 19.5% and in the February Vestkapp Box to 20.2% (Figs. 3.12 and 3.13). With a single exception, the females of the February Box and Gould Bay/

Vahsel Bay had a higher dry weight and, simultaneously, a higher lipid weight than females from the January Box, the weigths of which lie at the bottom end of the regression curve erected on the data from females caught later. Overall, the females of the January Vestkapp Box have a lower lipid/dry weight ratio.

The relationship between the weights of individual lipid classes and of total lipids also demonstrates the differences between Boxes. Weight of triglycerides increases more rapidly than that of phospholipids as total lipid weight rises, but the greatest increases are those of wax esters. All wax ester weights below 18 µg were found in animals from the January Box; triglycerides of these animals, at less than 12 µg, also were at the bottom end of the range. Wax esters from Vahsel Bay/Gould Bay and the February Vestkapp Box, weighing 18-49 µg were distinctly heavier. Triglycerides vary more (4-21 µg), but even here the higher values come from Vahsel Bay/Gould Bay and the February Box.

The precentage increase of lipids in females from Gould Bay/Vahsel Bay and the February Vestkapp Box is mirrored in the percentages of the lipid classes (Tab. 3.4 and Fig. 3.12): in the January Box, phospholipids (38.4%) predominate, whereas in the Filchner Depression there is a strong increase of wax esters (40.9%) and triglycerides (28.0%). Phospholipids make up only one quarter of the lipids. A comparison of the two Vestkapp Boxes also shows that phospholipids are decreased to a quarter, whereas the fraction of wax esters, i.e. storage lipids, nearly doubles to 52.3%. Even though total lipid

increase is not very great, there is a pronounced change in the composition of the lipids, the wax ester fraction growing the most. In comparison to the previously discussed herbivorous copepods (exception: ? R. gigas), the omnivorous species, Metridia gerlachei is characterized by overall low lipid content with a high phospholipid fraction.

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[For Table and Figures translated below, see following intercaletd pages]

Table 3.4. Station and Measurement Data for Metridia gerlachei copepodids C IV, C V, females (F); Weddell Sea 1985 (36)

Figure 3.12. Lipid content and Composition of Metridia gerlachei, Weddell Sea (C5: C V, F: females; V/G: Vahsel/Gould Bay (37)

Figure 3.13. Lipid Content of Metridia gerlachei during the Study Period (C V x, females •; linear regression)

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Euchaeta antarctica GIESBRECHT, 1902 (38)

Females and males of the Euchaeta species considered here all came from the Weddell Sea, and were identified as Euchaeta antarctica, but the speciation of the copepodid stages is uncertain. Inasmuch as E. antarctica is by far the most numerous of the Euchaeta species in the Weddell Sea, copepodids, often caught in great numbers, most probably belong to that species.

Table 3.5 and Figures 3.14-3.16 detail the data concerning Euchaeta. There were too few C III for reliable total lipid measurements, but lipid composition was determined: the three largest fractions are

Tab. 3.4. Stationsdaten und Messergebnisse von Metridia gerlachei Copepodite C4, C5, Females (F); Weddell See 1985

Stat. No.	Date D/M/Y	Haul Depth (m)	Stage C, F	Total Number (n)	Mean WetWt (g)	Mean DryWt (g)	Mean Lipid (g)	Total Lipid %WetWt	Total Lipid %DryWt	Lipid Class Composition in Percent of Total Lipid: Polar	Neutral	PE	PS+ PI	PC	SM+ LPC	WE+ SE	TAG	FFA	CHOL	DAG
255	23/01/85	225-0	C4	45						18.8	81.2	8.6	0.5	9.1	0.6	39.9	23.9	11.1	6.3	0.0
254	23/01/85	215-0	C5	76	0.00106	0.000082				18.3	81.7	7.2	0.3	8.7	2.0	43.5	25.6	7.5	5.1	0.0
264	25/01/85	220-0	C5	200	0.00101	0.000094	0.000023	2.2	24.1	24.7	75.3	12.4	1.0	9.4	1.8	40.6	22.2	7.3	5.1	0.0
269	26/01/85	210-0	C5	200	0.00099	0.000086	0.000014	1.4	16.7	33.0	67.0	16.0	0.5	15.6	0.9	36.8	22.7	3.0	4.5	0.0
Mean					0.00102	0.000087	0.000019	1.8	20.4	25.3	74.7	11.9	0.6	11.2	1.6	40.3	23.5	5.9	4.9	0.0
327	14/02/85	205-0	C5	110	0.00107	0.000069	0.000015	1.4	22.3	30.0	70.0	12.4	0.6	16.2	0.9	40.7	20.6	4.2	4.4	0.0
252	23/01/85	210-0	F	124	0.00243	0.000288	0.000045	1.8	15.6	31.3	68.7	13.5	0.3	16.4	1.1	36.6	19.3	5.4	5.5	1.9
254	23/01/85	215-0	F	80	0.00230	0.000273	0.000056	2.4	20.6	40.5	59.5	13.1	0.9	23.1	3.4	21.8	19.7	7.9	6.9	3.2
258	24/01/85	227-0	F	200	0.00273	0.000274	0.000044	1.6	15.9	29.3	70.7	12.0	0.8	14.2	2.4	37.5	20.9	6.7	5.6	0.0
262	25/01/85	175-0	F	200	0.00278	0.000335	0.000048	1.7	14.7	34.0	66.0	13.4	0.4	19.2	0.9	35.8	18.9	4.3	5.1	1.8
264	25/01/85	220-0	F	200	0.00232	0.000290	0.000042	1.8	14.3	44.9	55.1	17.4	0.8	23.1	3.6	18.4	17.9	8.8	6.7	3.3
269	26/01/85	210-0	F	199	0.00283	0.000328	0.000041	1.5	12.5	50.7	49.3	22.0	0.3	27.5	0.9	20.4	17.0	4.6	6.5	0.7
Mean					0.00257	0.000298	0.000046	1.8	15.6	38.4	61.5	15.2	0.6	20.6	2.1	28.4	18.9	6.3	6.1	1.8
299	05/02/85	240-0	F	200	0.00308	0.000341	0.000065	2.1	19.1	26.4	73.6	9.5	0.7	15.5	0.7	41.8	26.0	2.2	3.7	0.0
306	07/02/85	215-0	F	200	0.00245	0.000339	0.000073	3.0	21.5	25.4	74.6	11.0	0.6	12.8	1.0	43.5	25.8	2.0	3.4	0.0
307	08/02/85	230-0	F	200	0.00273	0.000339	0.000068	2.5	20.2	23.7	76.3	9.8	0.5	12.7	0.7	41.3	30.1	1.5	3.4	0.0
309	09/02/85	220-0	F	200	0.00233	0.000286	0.000050	2.1	17.3	25.8	74.2	12.9	0.2	12.1	0.7	37.1	30.2	2.1	4.7	0.0
Mean					0.00265	0.000326	0.000064	2.4	19.5	25.3	74.7	10.8	0.5	13.3	0.8	40.9	28.0	2.0	3.8	0.0
315	12/02/85	190-0	F	200	0.00263	0.000351	0.000066	2.5	18.8	25.0	75.0	11.9	0.2	12.4	0.5	47.5	21.4	1.7	4.4	0.0
318	12/02/85	205-0	F	200	0.00247	0.000344	0.000067	2.7	19.4	24.3	75.6	11.7	0.2	11.6	0.8	48.4	19.7	3.0	4.5	0.0
324	14/02/85	205-0	F	200	0.00240	0.000375	0.000077	3.2	20.6	26.6	73.4	12.9	0.2	13.1	0.3	46.5	21.9	0.9	4.1	0.0
336	16/02/85	180-0	F	200	0.00230	0.000384	0.000088	3.8	23.0	17.3	82.7	7.4	0.2	9.0	0.6	55.6	23.3	0.7	3.2	0.0
337	16/02/85	220-0	F	200	0.00276	0.000354	0.000066	2.4	18.5	29.3	70.7	14.0	0.1	14.5	0.7	60.3	5.7	2.1	2.5	0.0
349	21/02/85	165-0	F	200	0.00252	0.000321	0.000067	2.6	20.8	23.3	76.7	10.9	0.4	11.2	0.8	55.6	14.1	3.3	3.6	0.0
Mean					0.00251	0.000355	0.000072	2.9	20.2	24.3	75.7	11.5	0.2	12.0	0.6	52.3	17.7	2.0	3.7	0.0

315	12/02/85	190-0		200	0.00663	0.000331	0.000069	2.3	10.0	23.0	12.9	11.7	0.6	12.3	0.6	52.3	17.7	2.0	3.7	0.0
318	12/02/85	205-0	F	200	0.00247	0.000344	0.000067	2.7	19.4	24.3	75.6	11.7	0.2	11.9	0.8	48.4	19.7	3.0	4.5	0.0
324	14/02/85	205-0	F	200	0.00240	0.000375	0.000077	3.2	20.6	28.6	73.4	12.9	0.2	13.1	0.3	46.5	21.9	0.9	4.1	0.0
336	16/02/85	180-0	F	200	0.00230	0.000304	0.000068	3.8	23.0	17.3	82.7	7.4	0.2	9.0	0.6	55.6	23.3	0.7	3.2	0.0
337	16/02/85	220-0	F	200	0.00276	0.000354	0.000066	2.4	18.5	29.3	70.7	14.0	0.1	14.5	0.7	60.3	5.7	2.1	2.5	0.0
349	21/02/85	163-0	F	200	0.00252	0.000321	0.000067	2.6	20.8	23.3	76.7	10.9	0.4	11.2	0.8	55.6	14.1	3.3	3.6	0.0
	Mean				0.00251	0.000355	0.000072	2.9	20.2	24.3	75.7	11.5	0.2	12.0	0.6	52.3	17.7	2.0	3.7	0.0

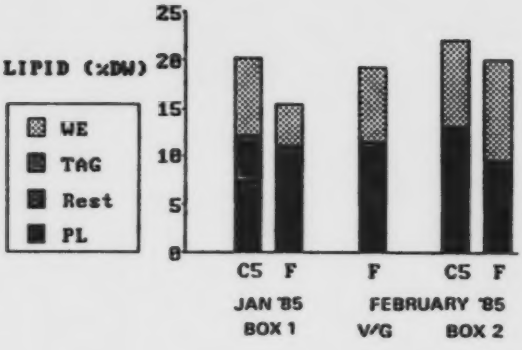

Abb. 3.12. Lipidgehalt und -zusammensetzung von *Metridia gerlachei*, Weddellmeer (C5: C5-Stadium, F: Weibchen; V/G: Vahsel/Gould Bay)

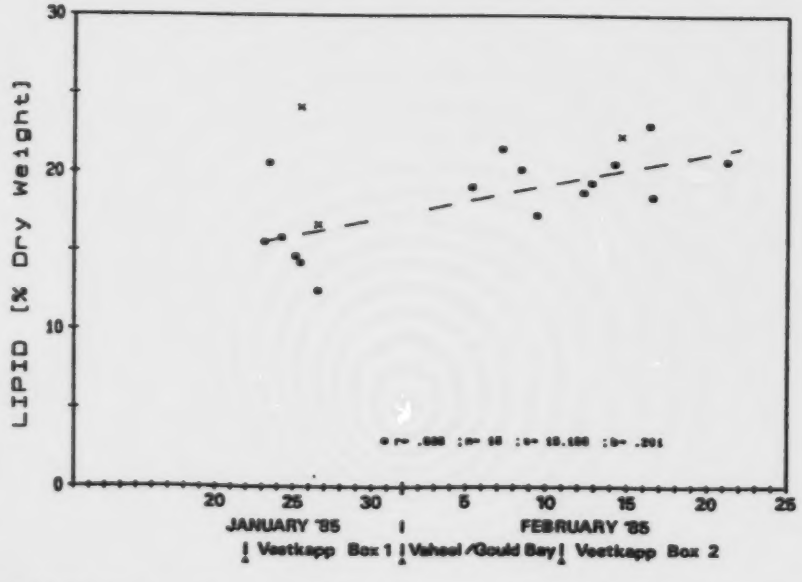

Abb. 3.13. Lipidgehalt von *Metridia gerlachei* im Verlaufe des Untersuchungszeitraums (C5 x, Weibchen •; lineare Regression)

wax esters (53.3%), triglycerides (18.1%) and phospholipids (19%). In the C IV lipid contents are 14%; wax esters (57%) and phospholipids (24.9%) increase their percentages slightly, while that of triglycerides (12.1%) decreases a little (Fig. 3.14). Data for C V and females are shown in Table 3.5 -- in reversed chronology -- in increasing order of dry weights. In light-weight C V from the February Vestkapp Box the percentage of total lipid increases with the dry weight (18.9-33.6%). The increase continues in C V from the Filchner Depression area in which the heaviest stages reach a lipid content of 45.1% (the maximum). At that stage, the fraction of wax esters increases also increases from about 64% to about 90%, linked to a clear decrease in the percentage of phospholipids (21.2-3.2%). Lipid contents in the females also remain high (36.8-42.0%), but lipid/dry weight ratio decreases at completion of C V (Fig. 3.15) -- possibly because of reproductive activities. Wax esters stabilize at very high levels (90.8-93.9%). The males of Euchaeta antarctica that we studied also showed high lipid content (36.7%) and extremely large wax ester fractions (95.9%) (Fig. 3.14). Seasonal trends in lipid accumulation could not be determined because of the paucity of data. An increase of lipid content in females of 4% within three weeks is not significant.

The relationship between the individual lipid classes (WE, PC, PE) and lipid contents is shown in Fig. 3.16. The increase in the lipid content is due to the wax esters, as already seen in C. acutus and R. R gigas. There is a clearly linear relationship. Phospholipids change little. We did not depict the lipid class

weight/dry weight ratios because such a graph would closely resemble Fig 3.15 insofar as wax esters are concerned, whereas phospholipids would show hardly any change. The linear increase of total lipids with dry weight is thus due primarily to the increase in wax esters.

In general, it would seem that in this carnivorous species lipid content and composition are linked directly to individual ontogeny, and in females to reproductive processes, but not to seasonal factors.

Euchirella rostromagna WOLFENDEDN, 1911

The relatively rare species, Euchirella rostromagna was represented only by females taken from the February Vestkapp Box (Tab. 3.6). On average, lipid contents were 26.7% of dry weight and the high fraction of triglycerides (77.9%) is remarkable. In opposition to this, wax esters represent only 8.7%, and their percentage decreases with rising lipid content, as does that of phospholipids (10.6%).

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[For Tables and Figures translated below see following intercalated pages]

Table 3.5. Station and Measurement Data for Euchaeta sp. C III (C3), C IV (C4), C V (C5) and Euchaeta antarctica females (F), males (M), sorted by stage and of d.w.; Weddell Sea 1985 (39)

Figure 3.14. Lipid Content and Composition of Euchaeta antarctica (C IV: C4, C5-1: C V Feb. Box, C5-2: C V [Vahsel/Gould Bay], F-1: females [Feb. Box], F-2: females [Jan. Box], F-3: females [Vahsel/Gould Bay], M: males [Vahsel/Gould Bay]; stages arranged in order of dry weight (40)

Figure 3.15. Lipid/Dry Weight Relationship in Euchaeta antarctica (Jan./Feb. 1985, Weddell Sea: C IV *, C V x; log-log regression; females ●; males v

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Figure 3.16. Lipid Classes (% d.w.)/ Lipid Contents of Euchaeta antarctica Weddell Sea: copepodids, females *, males ●; phosphatidylcholine o; phosphatidylethanolamine + (41)

Table 3.6. Station and Measurement Data of Euchirella rostramagna Females, sorted by Dry Weight; Weddell Sea

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3.2 Euphausiaceae (42)

Euphausia superba DANA 1850

Lipid analyses for Euphausia superba are given in Tables 3.7-3.10 and Figures 3.17-3.25. Total lipid data (Figs. 3.17-3.19) from October/ November 1983 (southern spring) from the region of the Antarctic Peninsula are rather homogeneously distributed over a wide range of body lenths (9-47 mm). At this time, krill have a rather low average lipid content of 8.7% (s = ±1.7) of dry weight. With increasing dry weight, lipid content decreases slightly but significantly (t-Test, $p < 0.05$; Fig. 3.17). In absolute terms, October/November 1983 lipids increase only slightly with increasing dry weight (Fig. 3.18).

These small lipid amounts are made up mostly of phospholipids (54.0%) and cholesterol (16.2%). The phospholipids are mainly phosphatidyl -choline and -ethanolamine. Krill's triglycerides, which are known to be storage lipids, average 9.8% and display large fluctuations, from 0% at a lipid content of 6.5%, to 28% when lipid content is 12%

Tab. 3.5. Stationsdaten und Messergebnisse von Euchaeta sp. Copepodite C3, C4, C5 und Euchaeta antarctica Females (F), Males (M), innerhalb der Stadien nach Trockengewicht sortiert; Weddell See 1985

Stat. No.	Date D/M/Y	Haul Depth (m)	Stage C,F,M	Total Number (n)	Mean WetWt (g)	Mean DryWt (g)	Mean Lipid (g)	Total Lipid %WetWt	Total Lipid %DryWt	Lipid Class Composition in Percent of Total Lipid: Polar	Neutral	PE	PS+ PI	PC	SM+ LPC	WE+ SE	TAG	FFA	CHOL	DAG
336	16/02/85	180-0	C3	8	0.0033	0.00011				19.0	81.0	5.3	0.0	12.1	1.5	53.3	18.1	5.5	4.2	0.0
336	16/02/85	180-0	C4	45	0.0047	0.00056	0.00008	1.7	14.0	24.9	75.0	7.9	0.4	15.3	1.3	57.0	12.1	3.1	2.9	0.0
336	16/02/85	180-0	C5	6	0.0106	0.00117	0.00022	2.1	18.9	21.2	78.8	8.3	0.8	11.1	1.1	64.2	7.9	3.6	2.9	0.2
339	16/02/85	205-0	C5	14	0.0160	0.00166	0.00033	2.1	20.0	13.4	86.6	4.6	0.6	7.6	0.6	77.0	5.3	1.6	2.1	0.7
349	21/02/85	165-0	C5	5	0.0134	0.00172	0.00058	4.3	33.6	6.3	93.6	2.2	0.0	3.3	0.7	87.2	4.5	0.6	1.3	0.0
Mean					0.0133	0.00152	0.00038	2.8	24.2	13.6	86.3	5.0	0.5	7.3	0.8	76.1	5.9	1.9	2.1	0.3
292	04/02/85	225-0	C5	57	0.0153	0.00279	0.00108	7.1	38.9	4.0	96.0	1.3	0.1	2.3	0.2	89.1	5.1	0.9	1.0	0.0
294	04/02/85	225-0	C5	72	0.0173	0.00303	0.00124	7.1	40.8	3.7	96.3	1.1	0.1	2.3	0.1	91.8	3.8	0.0	0.7	0.0
296	04/02/85	215-0	C5	60	0.0172	0.00363	0.00164	9.5	45.1	3.2	96.8	1.0	0.0	2.1	0.2	89.0	6.9	0.0	0.8	0.0
Mean					0.0166	0.00315	0.00132	7.9	41.6	3.6	96.4	1.1	0.1	2.2	0.2	90.0	5.3	0.3	0.8	0.0
349	21/02/85	165-0	F	4	0.0289	0.00474	0.00199	6.9	42.0	3.3	96.7	1.1	0.1	1.8	0.3	93.9	2.8	0.0	0.0	0.0
271	27/01/85	190-0	F	7	0.0293	0.00504	0.00191	6.5	38.0	4.3	95.7	1.3	0.1	2.7	0.3	90.8	3.1	1.1	0.8	0.0
294	04/02/85	225-0	F	12	0.0393	0.00562	0.00207	5.3	36.8	3.2	96.8	1.1	0.0	1.7	0.4	91.7	4.4	0.0	0.8	0.0
292	04/02/85	225-0	F	17	0.0316	0.00568	0.00225	7.1	39.6	3.7	96.3	1.2	0.0	2.0	0.5	91.3	3.5	0.8	0.7	0.0
296	04/02/85	215-0	F	8	0.0329	0.00572	0.00224	6.8	39.2											
Mean					0.0346	0.00567	0.00219	6.4	38.5	3.5	96.5	1.2	0.0	1.9	0.5	91.5	4.0	0.4	0.8	0.0
296	04/02/85	215-0	M	10	0.0165	0.00282	0.00096	5.9	34.2	3.8	96.2	1.3	0.1	2.0	0.4	95.4	0.0	0.0	0.8	0.0
294	04/02/85	225-0	M	5	0.0165	0.00299	0.00113	6.8	37.7											
292	04/02/85	225-0	M	26	0.0167	0.00321	0.00123	7.4	38.3	2.9	97.1	0.8	0.0	1.6	0.4	96.5	0.0	0.0	0.6	0.0
Mean					0.0165	0.00301	0.00111	6.7	36.7	3.4	96.6	1.1	0.1	1.8	0.4	95.9	0.0	0.0	0.7	0.0

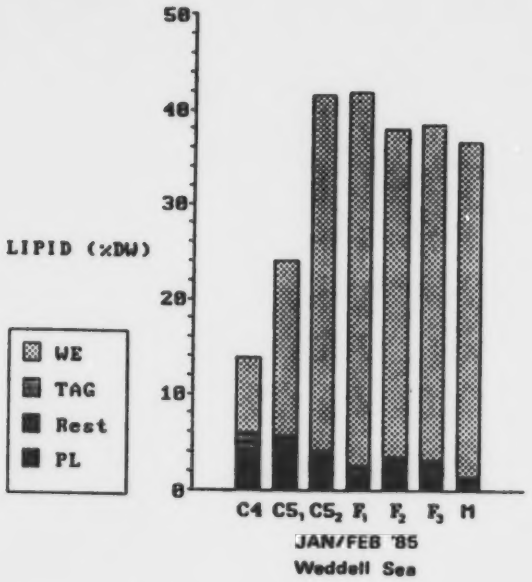

Abb. 3.14. Lipidgehalt und -zusammensetzung von *Euchaeta antarctica* (C4: C4-Stadium, $C5_1$: C5 (Feb.-Box), $C5_2$: C5 (Vahsel/Gould Bay), F_1: Weibchen (Feb.-Box), F_2: Weibchen (Jan.-Box), F_3: Weibchen (Vahsel/Gould Bay, M: Männchen (Vahsel/Gould Bay; Stadien nach Trockengewicht geordnet)

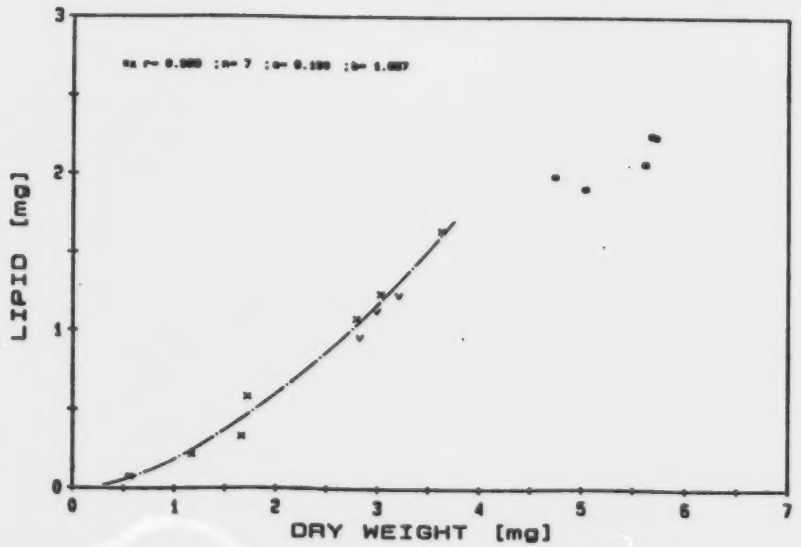

Abb. 3.15. Lipid-/Trockengewichtsbeziehung von *Euchaeta antarctica* (Jan./Feb. 1985, Weddellmeer: C4 *, C5 x, doppelt logarithmische Regression; Weibchen o; Männchen v;

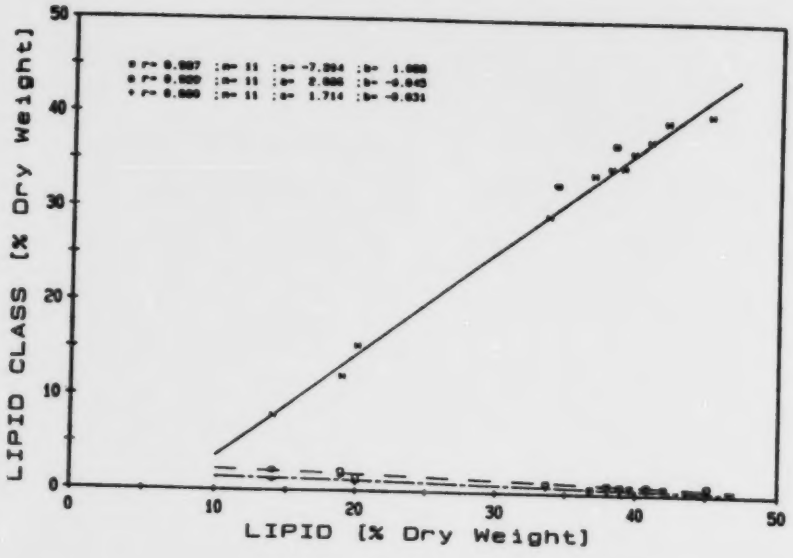

Abb. 3.16. Lipidklassen (% TG)/Lipidgehalt von *Euchaeta antarctica*, Weddellmeer: Wachsester: Copepodite, Weibchen *, Männchen •; Phosphatidylcholin o; Phosphatidylethanolamin +

rctica (C4: C4-Sta-
hen (Feb.-Box), F_3:
:hen (Vahsel/Gould

ica (Jan./Feb. 1985,
ıen •; Männchen v;

Tab. 3.6. Stationsdaten und Messergebnisse von Euchirella rostromagna Weibchen, nach Trockengewicht sortiert; Weddell See 1985

Stat. No.	Date D/M/Y	Haul Depth (m)	Total Number (n)	Mean WetWt (g)	Mean DryWt (g)	Mean Lipid (g)	Total Lipid %WetWt	Total Lipid %DryWt
342	17/02/85	405-200	7	0.0199	0.00320	0.00077	3.9	24.1
340	17/02/85	225-0	8	0.0153	0.00333	0.00096	6.3	28.8
340	17/02/85	520-200	12	0.0164	0.00356	0.00097	5.9	27.3
Mean				0.0172	0.00336	0.00090	5.4	26.7

Stat. No.	Lipid Class Composition in Percent of Total Lipid										
	Polar	Neutral	PE	PS+PI	PC	SM+LPC	WE+SE	TAG	FFA	CHOL	DAG
342	12.7	87.3	4.1	0.2	7.3	1.1	12.2	72.1	1.5	1.5	0.0
340	9.6	90.4	2.5	0.0	6.0	1.0	6.6	81.2	1.0	1.6	0.0
340	9.4	90.6	2.9	0.1	5.6	0.9	7.2	80.5	1.5	1.4	0.0
Mean	10.6	89.4	3.2	0.1	6.3	1.0	8.7	77.9	1.3	1.5	0.0

(Tab. 3.7). Figures 3.20 and 3.21 show the relationship between lipid classes (mg and % d.w.) and total lipid weight/lipid content: in opposition to phosphatidylethanolamine, phosphatidylcholine, and even more, triglycerides, clearly increase linearily with increasing total lipid weight or fraction.

Depending upon total lipid content, there is an inverse correlation between phospholipids and triglycerides (as % total lipid) (Figs. 3.22-3.24). The phospholipid fraction, in particular phosphatidyl-ethanolamine, decreases rapidly as lipid content (% d.w.) increases; contrariwise, triglycerides rise to a maxiumum of about 60%. In addition to phospholipids and triglycerides, the wax ester/sterol ester fraction (13.4%) is well represented in the October/November animals (Fig. 3.25); according to the literature, most of these lipids should be sterol esters.

At the beginning of January 1985, lipid contents are somewhat higher (11.7%, s = $\pm$5.2) (Tab. 3.8 and Figs. 3.17-3.19). The large individual fluctuations (5.5-23.6%) are apparently not determined only by the animal's sex. Organisms from Station 226 (northern Bransfield Strait) are, on average, "fatter" (16.1%), compared to a lipid content of 9.1% of those from a region northeast of Elephant Island (Stations 230, 238).

The inverse correlation, dependent upon lipid content, between phospholipids and triglycerides (in % total lipid) (Figs. 3.22-3.24) is illustrated by the somewhat lower, average phospholipid fraction

(47.5%) and a triglyceride fraction (21.9%) that is nearly double that of the October animals (Fig. 3.25). Cholesterol (average 11.2%) and wax ester (9.5%) fractions are somewhat lower. In four cases, free fatty acids were present in a disquietingly high (? autolysis) fraction of 15-20%.

Samples from the southern Weddell Sea (February Vestkapp Box) made possible, for the first time, study of lipids from early larval stages of E. superba (calyptopis I, II) (Tab. 3.9). Total lipids in calyptopis I are 11.6%, increase to 14.4% in calyptopis II. At both stages, phospholipids make up about 30% of total lipids (Fig. 3.25); but triglycerides change (C I: 42.8%; C II: 30.0%), as do wax/sterol esters (C I: 16.2%; C II: 31.1%). Unfortunately, later larval stages (furcilia, postlarva) are missing.

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[For Figures and Plates translated below, see following intercalated pages]

Table 3.7. Station and Measurement Data of E. superba, sorted according to d. w.; Antarctic Peninsula 1983 (43)

Table 3.8. Station and Measurement Data of E. superba, sorted according to d. w.; Antarctic Peninsula 1985 (44)

Table 3.9 Station and Measurement Data of E. superba larvae, sorted according to d. w.; calyptopis I + II (C-I+C-2); Vestkapp Box 2, Weddell Sea 1985 (45)

Table 3.10. Station and Measurement Data of E. superba (subadult, adult), according to d. w.; Weddell Sea 1985 (46)

Figure 3.17. Lipid Content/Dry Weight Relation in Euphausia superba (x: Oct./Nov. 1983, Antarctic Peninsula; linear regression; o: Jan. 1985, Antarctic Peninsula; *: Jan./Feb. 1985, Weddell Sea; log-log regression (47)

Figure 3.18. Lipid Weight/Dry Weight Relation of Euphausia superba (x: Oct./Nov. 1983, Antarctic Peninsula; linear regression; o: Jan. 1985, Antarctic Peninsula; *: Jan./Feb. 1985, Weddell Sea; log-log regression

Figure 3.19. Lipid Content of Euphausia superba During Study: calyptopis I and II +, subadult and adult xo* (48)

Figure 3.20. Lipid Class/Total Lipid Weights in Euphausia superba (Antarctic Peninsula, Weddell Sea): triglycerides +; phosphatidylcholine o; phosphatidylethanolamine *; linear regression

Figure 3.21. Lipid Classes (% d.w.) Lipids in Euphausia superba (Antarctic Peninsula, Weddell Sea): triglyceride +, phosphatidylcholine o, phosphatidylethanolamine *, linear regression (49)

Figure 3.22. Phospholipid (% lipid)/Lipid Content of Euphausia superba (x: Oct./Nov. 1983, Antarctic Peninsula; o: Jan. 1985, Antarctic Peninsula; *: Jan./Feb. 1985, Weddell Sea; log-log regression

Figure 3.23. Phosphatidylcholine/-ethanolamine (% Total Lipid)/Lipid Content in Euphausia superba (phosphatidylcholine o, linear regression; phosphatidylethanolamine *; log-log regression (50)

Figure 3.24. Triglycerides (% Lipid)/Lipid Content in Euphausia superba (x: Oct./Nov. 1983, Antarctic Peninsula; o: Jan. 1985, Antarctic Peninsula; * Jan./Feb. 1985, Weddell Sea; data fitted to a parabola)

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The few subadults and adults of E. superba (19-56 mm) from the southern Weddell Sea (Tab. 3.10; Figs. 3.17-3.19) have a much higher lipid content (26.8%, s = ±6.5) then their conspecific mates from (51)

Tab. 3.7. Stationsdaten und Messergebnisse von E. superba, nach Trockengewicht sortiert; Antarktische Halbinsel 1983

Stat. No.	Date D/M/Y	Haul Depth (m)	Total Number (n)	Approx. Length (mm)	Mean WetWt (g)	Mean DryWt (g)	Mean Lipid (g)	Total Lipid %WetWt	Total Lipid %DryWt	Lipid Class Composition in Percent of Total Lipid: Polar	Neutral	PE	PS+PI	PC	SM+LPC	WE+SE	TAG	FFA	CHOL	DAG
118	29/10/83	100-0	10	10-12	0.0092	0.0016	0.00016	1.7	10.2	59.2	40.7	19.8	1.1	37.8	0.6	6.7	6.2	7.5	20.3	0.0
118	29/10/83	100-0	10	9-12	0.0097	0.0016	0.00015	1.5	9.5											
118	29/10/83	100-0	10	10-13	0.0116	0.0020	0.00017	1.5	8.5											
198	09/11/83	200-0	10	10-13	0.0120	0.0020	0.00018	1.5	8.8	58.2	41.8	22.6	2.1	32.1	1.6	10.3	7.1	7.6	16.7	0.0
198	09/11/83	200-0	10	12-16	0.0198	0.0033	0.00038	1.9	11.6	56.8	43.2	17.8	1.3	36.9	0.9	10.4	15.9	5.2	11.6	0.0
198	09/11/83	200-0	10	16-19	0.0389	0.0073	0.00083	2.1	11.4											
118	29/10/83	100-0	10	18-23	0.0514	0.0093	0.00105	2.1	11.3											
116	28/10/83	40-0	1	22	0.0746	0.0121	0.00120	1.6	10.0	50.3	49.7	13.6	0.4	35.8	0.6	9.6	24.2	5.8	10.1	0.0
116	28/10/83	40-0	1	26	0.1005	0.0162	0.00145	1.4	9.0	47.8	52.2	13.3	1.2	31.1	2.2	11.9	6.5	12.2	21.5	0.0
202	09/11/83	200-0	1	28	0.1334	0.0175	0.00178	1.3	10.2	54.6	45.4	19.2	0.7	32.9	1.8	10.6	5.3	7.8	21.8	0.0
118	29/10/83	100-0	1	28	0.1381	0.0232	0.00259	1.9	11.2	42.4	57.6	13.1	0.3	28.1	0.8	30.8	2.2	6.5	18.2	0.0
116	28/10/83	40-0	1	30	0.1702	0.0234	0.00166	1.0	7.1	49.9	50.1	15.4	0.1	33.8	0.6	18.8	16.0	4.3	10.9	0.0
116	28/10/83	40-0	1	32	0.2079	0.0305	0.00277	1.3	9.1	55.3	44.7	20.5	0.3	33.0	1.5	10.3	4.6	6.9	22.8	0.0
202	09/11/83	200-0	1	29	0.1719	0.0311	0.00369	2.1	11.9											
154	05/11/83	200-0	1	32	0.2529	0.0331	0.00266	1.1	8.0											
154	05/11/83	200-0	1	33	0.2581	0.0334	0.00267	1.0	8.0	53.2	46.8	15.9	1.1	35.0	1.1	18.5	6.9	5.2	16.8	0.0
202	09/11/83	200-0	1	32	0.2164	0.0372	0.00383	1.8	10.3											
116	28/10/83	40-0	1	36	0.3073	0.0404	0.00275	0.9	6.8											
202	09/11/83	200-0	1	31	0.2239	0.0409	0.00404	1.8	9.9	47.8	52.2	15.6	0.1	30.4	1.6	18.6	2.1	8.7	22.8	0.0
116	28/10/83	40-0	1	34	0.2666	0.0441	0.00414	1.6	9.4											
154	05/11/83	200-0	1	35	0.3112	0.0450	0.00345	1.1	7.7											
116	28/10/83	40-0	1	40	0.3460	0.0553	0.00400	1.2	7.2											
154	05/11/83	200-0	1	37	0.3782	0.0555	0.00436	1.2	7.9	52.1	47.9	16.5	0.3	33.7	1.6	17.9	2.2	7.3	20.5	0.0
202	09/11/83	200-0	1	34	0.3279	0.0567	0.00558	1.7	9.8											
154	05/11/83	200-0	1	38	0.3750	0.0602	0.00447	1.2	7.4	49.3	50.7	9.8	0.8	37.8	1.0	11.4	20.5	8.0	10.7	0.0
116	28/10/83	40-0	1	38	0.4233	0.0621	0.00432	1.0	7.0											
154	05/11/83	200-0	1	40	0.4478	0.0623	0.00417	0.9	6.7											
202	09/11/83	200-0	1	37	0.3988	0.0652	0.00785	2.0	12.0	58.9	41.1	21.8	0.0	36.4	0.7	13.3	4.9	6.3	16.5	0.0
202	09/11/83	200-0	1	38	0.4138	0.0769	0.00706	1.7	9.2	47.0	53.0	9.1	0.2	37.6	0.1	11.8	28.2	4.2	8.8	0.0
116	28/10/83	40-0	1	42	0.5041	0.0778	0.00695	1.4	8.9											
202	09/11/83	200-0	1	39	0.4603	0.0813	0.00657	1.4	8.1	52.6	47.4	12.9	0.0	39.2	0.6	11.6	21.1	3.6	11.0	0.0
154	05/11/83	200-0	1	42	0.5960	0.0831	0.00536	0.9	6.5											
202	09/11/83	200-0	1	42	0.4975	0.0897	0.00614	1.2	6.8											
154	05/11/83	200-0	1	43	0.5440	0.0931	0.00724	1.3	7.8											
116	28/10/83	40-0	1	44	0.6627	0.0958	0.00609	0.9	6.4	57.3	42.7	22.2	0.5	33.4	1.2	13.6	5.0	6.4	17.8	0.0
154	05/11/83	200-0	1	45	0.6572	0.0997	0.00644	1.0	6.5											
202	09/11/83	200-0	1	44	0.6665	0.1128	0.00735	1.1	6.5	59.7	40.3	25.7	0.3	32.2	1.4	13.2	0.0	8.8	18.4	0.0
116	28/10/83	40-0	1	46	0.8170	0.1221	0.00838	1.0	6.9	62.4	37.6	21.4	0.4	39.7	1.0	9.4	9.8	5.1	13.2	0.0
154	05/11/83	200-0	1	47	0.7877	0.1330	0.00925	1.2	7.0	64.3	35.7	19.7	1.1	42.5	1.0	9.5	6.5	5.3	14.4	0.0
Mean								1.4	8.7	54.0	46.0	17.3	0.6	35.0	1.1	13.4	9.8	6.6	16.2	0.0
Std.Dev.								0.4	1.7	5.7	5.7	4.5	0.5	3.5	0.5	5.4	8.2	2.0	2.0	0.0

Tab. 3.8. Stationsdaten und Messergebnisse von E. superba, nach Trockengewicht sortiert; Antarktische Halbinsel 1985

Stat. No.	Date D/M/Y	Haul Depth (m)	Total Number (n)	Approx. Length (mm)	Sex F,M	Mean WetWt (g)	Mean DryWt (g)	Mean Lipid (g)	Total Lipid %WetWt	Total Lipid %DryWt	Lipid Class Composition in Percent of Total Lipid: Polar	Neutral	PE	PS+PI	PC	SM+LPC	WE+SE	TAG	FFA	CHOL	DAG
226	07/01/85	50-0	1	27		0.1386	0.0267	0.0031	2.2	11.6	44.8	55.2	11.0	0.1	32.5	1.2	12.1	11.1	19.9	8.2	3.8
230	09/01/85	100-0	1	31		0.2161	0.0380	0.0030	1.4	7.9	48.1	51.9	18.7	0.0	28.1	1.3	16.2	12.3	6.8	14.1	2.5
226	07/01/85	50-0	1	32		0.2375	0.0415	0.0071	3.0	17.1	40.2	59.8	4.1	0.2	35.6	0.3	7.3	29.4	11.2	5.3	6.5
230	09/01/85	100-0	1	33		0.2749	0.0463	0.0037	1.4	8.1	42.6	57.4	15.4	0.1	26.0	1.1	19.9	13.5	7.5	12.7	3.8
226	07/01/85	50-0	1	33		0.2659	0.0477	0.0030	1.1	6.3	54.9	45.1	17.3	0.0	36.2	1.4	8.4	6.5	16.9	13.4	0.0
226	07/01/85	50-0	1	33		0.2641	0.0485	0.0080	3.0	16.4	41.3	58.7	5.2	0.2	35.8	0.3	7.4	25.1	13.0	5.9	7.3
226	07/01/85	50-0	1	33		0.2836	0.0571	0.0091	3.2	16.0											
230	09/01/85	100-0	1	34		0.3056	0.0654	0.0131	4.3	20.0	36.4	63.6	3.7	0.2	32.4	0.3	7.9	42.5	1.8	6.3	5.0
226	07/01/85	50-0	1	36		0.3248	0.0740	0.0121	3.7	16.3	40.3	59.7	4.2	0.1	35.4	0.5	7.5	24.3	17.6	5.4	5.2
230	09/01/85	100-0	1	39		0.4404	0.0770	0.0073	1.7	9.4											
230	09/01/85	100-0	1	44	M	0.5720	0.0904	0.0060	1.1	6.6	48.3	51.7	17.9	0.0	28.9	1.5	10.1	11.2	9.4	18.8	2.1
226	07/01/85	50-0	1	37		0.4117	0.0936	0.0193	4.7	20.7											
226	07/01/85	50-0	1	39		0.4677	0.0953	0.0225	4.8	23.6	36.5	63.5	1.6	0.0	34.6	0.2	5.3	40.5	8.1	4.1	5.5
230	09/01/85	100-0	1	43	F	0.6430	0.1008	0.0085	1.3	8.4											
230	09/01/85	100-0	1	45	F	0.7025	0.1232	0.0134	1.9	10.9	44.0	56.0	7.9	0.0	35.5	0.6	10.4	29.0	2.3	10.5	3.8
230	09/01/85	100-0	1	44	F	0.6961	0.1244	0.0094	1.4	7.6	45.9	54.1	12.6	0.0	32.7	0.6	9.7	24.7	3.2	12.1	4.4
226	07/01/85	50-0	1	42		0.6032	0.1341	0.0235	3.9	17.5	39.9	60.1	4.0	0.0	35.8	0.1	6.1	32.9	9.7	5.8	5.6
238	11/01/85	80-0	1	46	M	0.7981	0.1519	0.0140	1.8	9.2	51.5	48.4	11.9	0.0	39.2	0.5	8.7	25.4	2.3	12.1	0.0
238	11/01/85	80-0	1	49	M	0.9081	0.1630	0.0095	1.0	5.8	67.7	32.3	29.7	0.0	37.4	0.7	9.9	4.1	0.0	18.3	0.0
238	11/01/85	80-0	1	51	F	1.0999	0.1789	0.0177	1.6	9.9	46.9	53.2	11.4	0.0	35.2	0.4	7.0	30.2	0.4	12.1	3.4
230	09/01/85	100-0	1	47	M	1.0324	0.1810	0.0174	1.7	9.6	39.1	60.9	9.6	0.0	28.2	1.2	12.2	28.4	8.1	12.2	0.0
238	11/01/85	80-0	1	49	F	0.9179	0.1831	0.0234	2.5	12.7	42.8	57.2	7.0	0.0	35.4	0.3	7.1	39.2	0.0	7.9	3.0
238	11/01/85	80-0	1	52	M	1.0897	0.1929	0.0113	1.0	5.8	64.1	35.9	28.9	0.0	34.2	0.9	11.2	0.0	1.7	23.0	0.0
226	07/01/85	50-0	1	46	F	0.8664	0.2004	0.0309	3.6	15.4	40.0	60.0	4.0	0.0	35.5	0.5	5.8	27.1	16.0	6.2	5.0
238	11/01/85	80-0	1	53	F	1.2564	0.2080	0.0250	2.0	12.0	46.7	53.3	5.8	0.1	40.5	0.3	7.2	37.3	0.0	8.8	0.0
238	11/01/85	80-0	1	56	M	1.3739	0.2508	0.0137	1.0	5.5	66.1	33.9	20.0	0.0	44.6	1.5	10.7	0.0	4.4	18.8	0.0
238	11/01/85	80-0	1	56	F	1.3466	0.2747	0.0163	1.2	5.9	65.5	34.6	20.1	0.5	43.6	1.2	9.6	8.3	1.1	15.6	0.0
Mean									2.3	11.7	47.5	52.5	11.8	0.1	34.9	0.7	9.5	21.9	7.0	11.2	2.9
Std.Dev.									1.2	5.2	9.7	9.7	8.0	0.1	4.5	0.5	3.4	13.1	6.3	6.3	2.5

238	11/01/85	80-0	1	56	F	1.3466	0.2747	0.0163	1.2	5.9	65.5	34.6	20.1	0.5	43.6	1.2	9.6	8.3	1.1	15.6	0.0
Mean									2.3	11.7	47.5	52.5	11.8	0.1	34.9	0.7	9.5	21.9	7.0	11.2	2.9
Std.Dev.									1.2	5.2	9.7	9.7	8.0	0.1	4.5	0.5	3.4	13.1	6.3	6.3	2.5

Tab. 3.9. Stationsdaten und Messergebnisse von E. superba-Larven, Calyptopis 1+2 (C1+C2), nach Trockengewicht sortiert; Vestkapp Box 2, Weddell See 1985

Stat. No.	Date D/M/Y	Haul Depth (m)	Stage C1,C2	Total Number (n)	Mean WetWt (g)	Mean DryWt (g)	Mean Lipid (g)	Total Lipid %WetWt	Total Lipid %DryWt	Lipid Class Composition in Percent of Total Lipid: Polar	Neutral	PE	PS+PI	PC	SM+LPC	WE+SE	TAG	FFA	CHOL	DAG
343	18/02/85	198-0	C1	400	0.00057	0.000050	0.0000061	1.1	12.0	26.6	73.4	9.4	0.0	17.0	0.2	17.2	47.6	1.1	7.5	0.0
349	21/02/85	165-0	C1	400	0.00055	0.000054	0.0000063	1.1	11.7	31.1	68.8	10.7	0.0	20.2	0.2	16.9	42.7	1.8	6.4	1.1
315	12/02/85	190-0	C1	400	0.00054	0.000058	0.0000069	1.3	11.9	36.5	63.5	12.6	0.0	23.7	0.2	16.1	38.7	1.8	6.9	0.0
315	12/02/85	190-0	C1	400	0.00061	0.000062	0.0000064	1.0	10.3	35.0	65.0	11.3	0.0	23.5	0.3	14.1	41.5	2.1	7.2	0.0
336	16/02/85	180-0	C1	400	0.00060	0.000065	0.0000083	1.4	12.7	32.3	67.7	9.2	0.0	22.9	0.2	13.6	45.2	2.0	6.9	0.0
345	18/02/85	225-0	C1	400	0.00061	0.000067	0.0000076	1.2	11.4	29.8	70.2	9.7	0.0	20.0	0.2	19.2	41.1	3.1	6.8	0.0
Mean					0.00058	0.000059	0.0000069	1.2	11.6	31.9	68.1	10.5	0.2	21.2	0.2	16.2	42.8	2.0	7.0	0.2
336	16/02/85	180-0	C2	105	0.00078	0.000089	0.0000124	1.6	13.8	28.5	71.5	10.0	0.0	18.4	0.1	30.8	33.5	0.0	7.1	0.0
349	21/02/85	165-0	C2	100	0.00101	0.000105	0.0000156	1.5	14.9	31.3	68.7	8.9	0.0	22.2	0.2	31.4	26.4	2.5	6.7	1.6
Mean					0.00090	0.000097	0.0000140	1.6	14.4	29.9	70.1	9.5	0.2	20.3	0.2	31.1	30.0	1.3	6.9	0.8

Tab. 3.10. Stationsdaten und Messergebnisse von E. superba (subadult, adult), nach Trockengewicht sortiert; Weddell See 1985

Stat. No.	Date D/M/Y	Haul Depth (m)	Total Number (n)	Approx. Length (mm)	Sex F,M	Mean WetWt (g)	Mean DryWt (g)	Mean Lipid (g)	Total Lipid %WetWt	Total Lipid %DryWt	Lipid Class Composition in Percent of Total Lipid: Po-lar	Neu-tral	PE	PS+ PI	PC	SM+ LPC	WE+ SE	TAG	FFA	CHOL	DAG
324	14/02/85	205-0	1	19		0.0617	0.0105	0.0029	4.7	27.4	37.0	62.9	6.2	0.0	30.6	0.3	18.5	34.1	4.0	6.3	0.0
324	14/02/85	205-0	1	26		0.1234	0.0272	0.0075	6.1	27.5	33.7	66.3	2.6	0.2	30.7	0.3	11.1	44.8	1.8	4.9	3.6
324	14/02/85	205-0	1	28		0.1593	0.0355	0.0099	6.2	28.0	32.7	67.3	2.1	0.1	30.3	0.3	9.7	49.0	1.7	4.1	2.8
323	13/02/85	205-0	1	30		0.2278	0.0390	0.0102	4.5	26.1	34.3	65.7	2.0	0.2	31.9	0.3	10.3	46.7	1.6	5.0	2.1
279	29/01/85	300-185	1	40		0.4930	0.0955	0.0238	4.8	24.9	35.3	64.7	1.8	0.0	33.0	0.5	6.5	47.3	2.6	5.4	2.9
279	29/01/85	300-185	1	41		0.5165	0.1006	0.0255	4.9	25.4											
324	14/02/85	205-0	1	41	F	0.5140	0.1040	0.0186	3.6	17.9											
358	24/02/85	400-0	1	45	M	0.6246	0.1350	0.0337	5.4	25.0	32.7	67.3	1.6	0.0	30.9	0.3	6.7	54.9	0.0	5.6	0.0
358	24/02/85	400-0	1	42	F	0.7181	0.1444	0.0475	6.6	32.9	33.8	66.2	1.0	0.0	32.7	0.1	4.4	57.7	0.0	4.1	0.0
358	24/02/85	400-0	1	43	F	0.6304	0.1456	0.0500	7.9	34.3	31.8	68.2	0.9	0.0	30.8	0.1	4.3	52.3	1.9	5.2	4.4
358	24/02/85	400-0	1	43	M	0.6761	0.1482	0.0489	7.2	33.0	33.8	66.1	1.0	0.0	32.7	0.1	4.5	56.4	0.0	5.2	0.0
279	29/01/85	300-185	1	44	F	0.6691	0.1601	0.0561	8.4	35.1											
358	24/02/85	400-0	1	44	M	0.8108	0.1641	0.0443	5.5	27.0	34.8	65.2	1.4	0.0	33.3	0.1	5.6	53.6	1.5	4.5	0.0
280	30/01/85	300-200	1	46	F	0.7756	0.1746	0.0474	6.1	27.1											
355	22/02/85	205-0	1	48	F	0.8280	0.1755	0.0329	4.0	18.7	29.1	70.9	3.3	0.1	25.6	0.2	6.2	53.2	3.5	5.4	2.5
358	24/02/85	400-0	1	47	F	0.7783	0.1764	0.0563	7.2	31.9	31.9	68.1	0.7	0.0	31.0	0.2	4.2	57.5	1.7	4.8	0.0
358	24/02/85	400-0	1	46	M	0.8336	0.1838	0.0604	7.2	32.9	32.4	67.6	1.4	0.0	30.9	0.1	4.1	53.1	0.9	5.3	4.2
280	30/01/85	300-200	1	47	M	0.8664	0.1866	0.0245	2.8	13.1	47.4	52.6	8.1	0.1	38.9	0.3	9.3	33.1	0.0	8.2	2.1
280	30/01/85	300-200	1	43	F	0.8056	0.1968	0.0670	8.3	34.0	36.0	64.0	1.0	0.1	34.7	0.1	3.9	55.1	1.6	3.3	0.0
279	29/01/85	300-185	1	56	M	1.2050	0.2815	0.0407	3.4	14.5	41.9	58.1	4.8	0.2	36.5	0.4	5.5	38.6	2.8	7.0	4.2
Mean									5.7	26.8	34.9	65.1	2.5	0.1	32.2	0.2	7.2	49.2	1.6	5.3	1.8
Std.Dev.									1.7	6.5	4.3	4.3	2.1	0.1	3.0	0.1	3.9	8.0	1.2	1.2	1.8

Page 53d

Abb. 3.18. L
1983, Antarkt
■: Jan./Feb. 1

LIPID [mg]

Abb. 3.17.
Nov. 1983,
inset; ■: Jan.

LIPID [% Dry Weight]

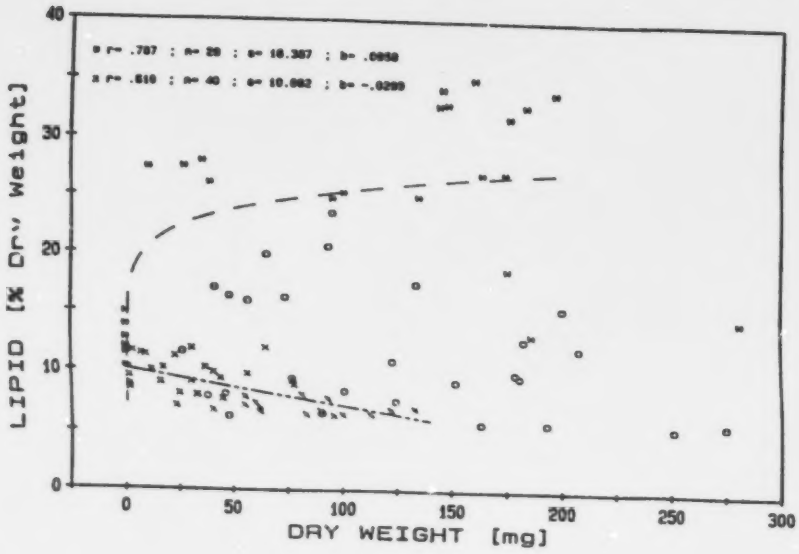


Abb. 3.17. Lipidgehalts-/Trockengewichtsbeziehung von *Euphausia superba* (x: Okt./Nov. 1983, Antarktische Halbinsel, lineare Regression; o: Jan. 1985, Antarktische Halbinsel; ∗: Jan./Feb. 1985, Weddellmeer, doppelt logarithmische Regression)

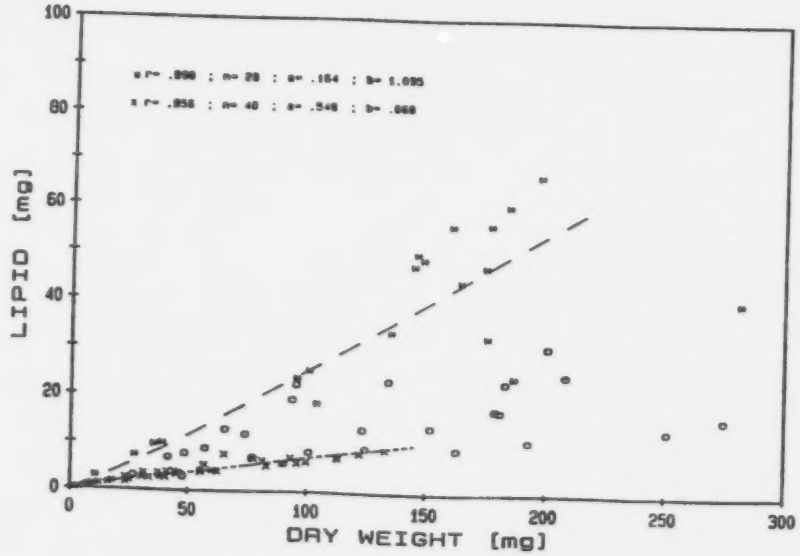


Abb. 3.18. Lipid-/Trockengewichtsbeziehung von *Euphausia superba* (x: Okt./Nov. 1983, Antarktische Halbinsel, lineare Regression; o: Jan. 1985, Antarktische Halbinsel; ∗: Jan./Feb. 1985, Weddellmeer, doppelt logarithmische Regression)

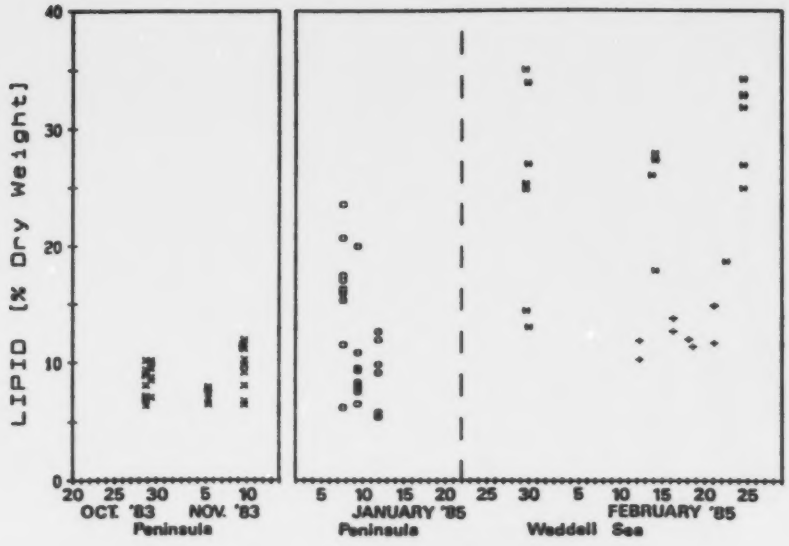


Abb. 3.19. Lipidgehalt von *Euphausia superba* im Verlauf des Untersuchungszeitraums: Calyptopis 1 und 2 +, Subadulte und Adulte x⊠

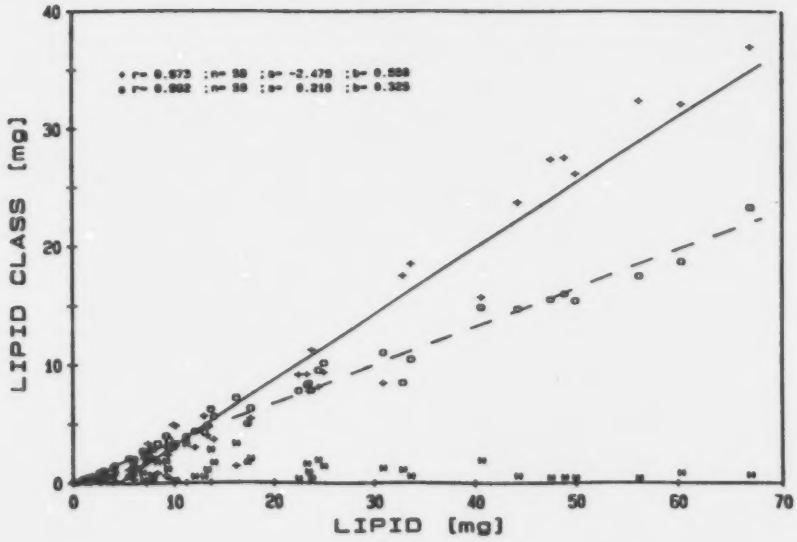


Abb. 3.20. Lipidklassengewicht/Gesamtlipidgewicht von *Euphausia superba* (Antarktische Halbinsel, Weddellmeer): Triglycerid +; Phosphatidylcholin o; Phosphatidylethanolamin ⊠; lineare Regression

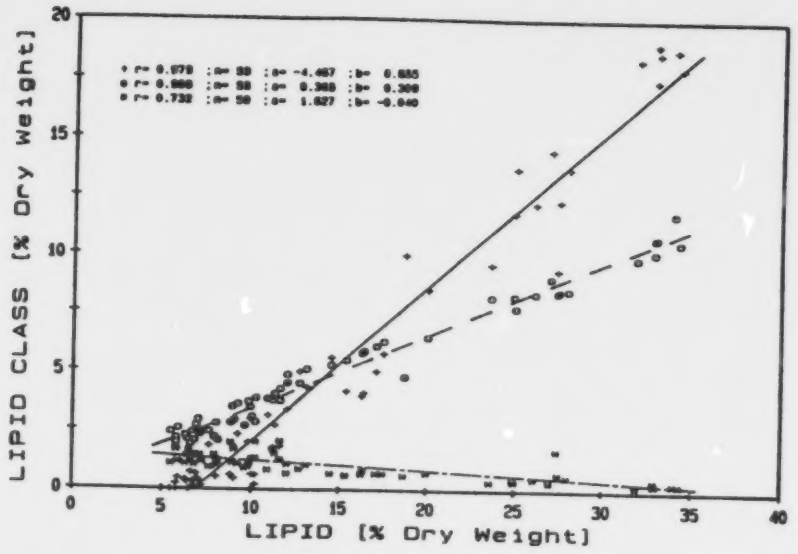


Abb. 3.21. Lipidklassen (% TG)/Gesamtlipidgehalt von *Euphausia superba* (Antarktische Halbinsel, Weddellmeer): Triglycerid +; Phosphatidylcholin o; Phosphatidylethanolamin *; lineare Regression

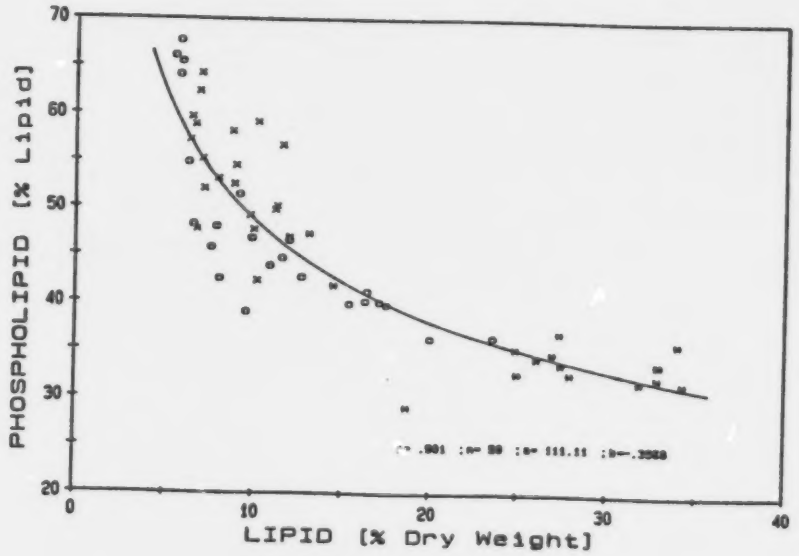


Abb. 3.22. Phospholipid (% Lipid)/Lipidgehalt von *Euphausia superba* (x: Okt./Nov. 1983, Antarktische Halbinsel; o: Jan. 1985, Antarktische Halbinsel; *: Jan./Feb. 1985, Weddellmeer; doppelt logarithmische Regression)

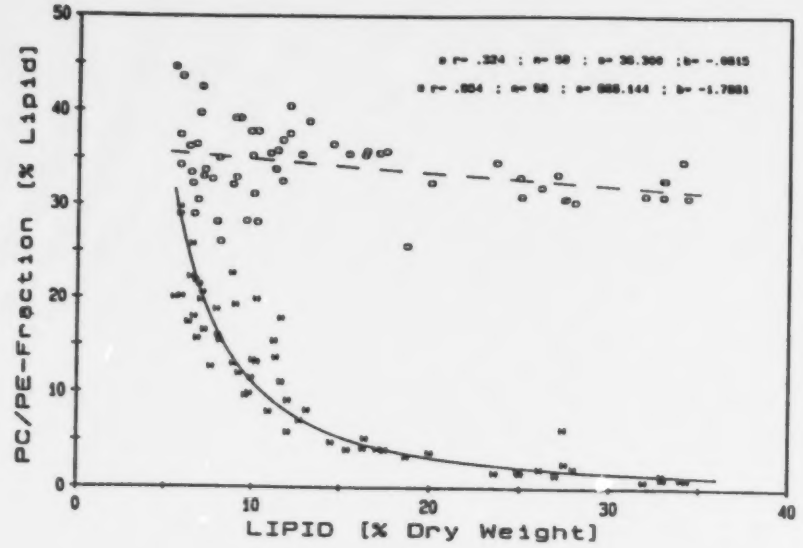


Abb. 3.23. Phosphatidylcholin bzw. -ethanolamin (% Lipid)/Lipidgehalt von *Euphausia superba* (Phosphatidylcholin o, lineare Regression; Phosphatidylethanolamin *, doppelt logarithmische Regression)

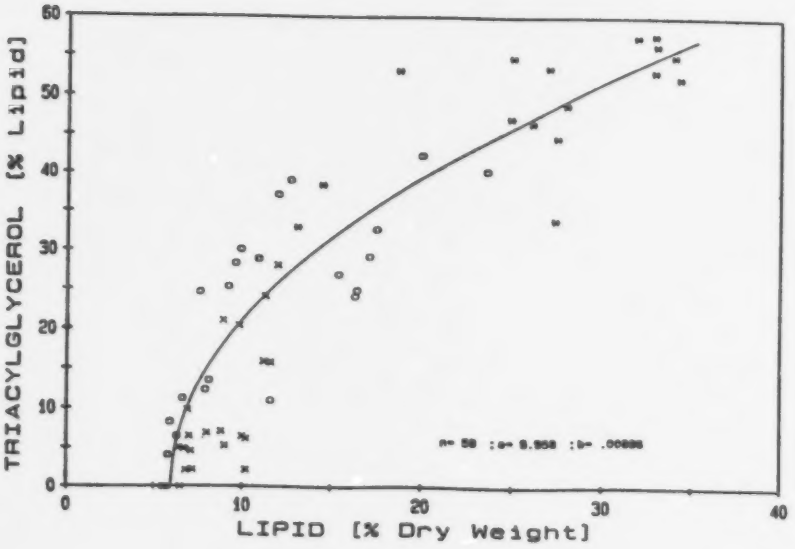
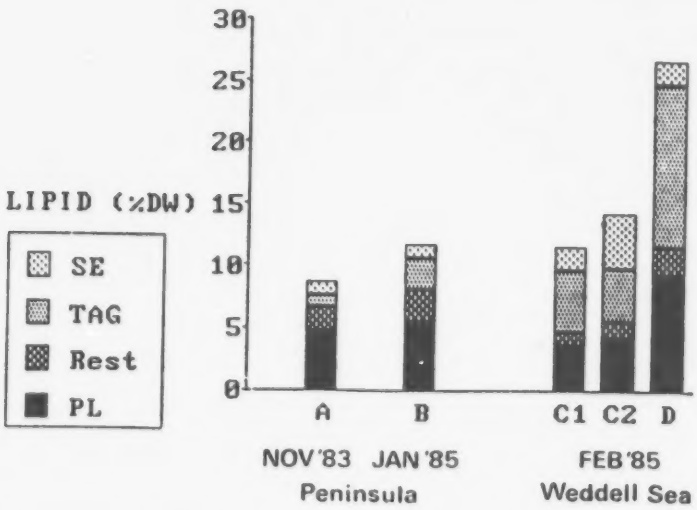


Abb. 3.24. Triglycerid (% Lipid)/Lipidgehalt von *Euphausia superba* (x: Okt./Nov. 1983, Antarktische Halbinsel; o: Jan. 1985, Antarktische Halbinsel; *: Jan./Feb. 1985, Weddellmeer; Meßwerte an Parabel angepaßt)

the Antarctic Peninsula, but variability is great (13-35%). Lowest levels were found in males of the Vestkapp January Box, but there were also females with low (below 20%) lipid contents, and males with more than 30%. Phospholipids (34.9%) and triglycerides (49.2%) account for 84% of lipids, whereas wax-/sterol esters only for 7.2% (Fig. 3.25). Phospholipids -- particularly, phosphatidylethanolamine -- occur in lower percentages in organisms of the Weddell Sea than in those of the Antarctic Peninsula. On the other hand, the triglyceride fraction is nearly twice as large in the south and, in animals caught after the 14th of February, measured, on average, 55%.

Figure 3.25. Lipid Content and Composition in Euphausia superba (A: 9-47 mm, B: 27-56 mm; C-1: calyptopis I; C-2: calyptopis II; D: 19-56 mm)



Euphausia crystallorophias HOLT and TATTERSALL, 1906 (52)

All of the early calyptopis and furcilia stages, right up to adults of Euphausia crystallorophias were available for lipid analyses (Figs. 3.26-3.31). Table 3.11 lists data for early larval and post-larval stages (according to d.w.). Analyses of subadult and adult E. crystallorophias are given in Tables 3.12-3.14, chronologically, for the January Vestkapp Box, Filchner Depression and the February Vestkapp Box. Lipid contents in calyptopis and furcilia measure on average 14.5% (d.w.) then rise to 22.7% in the postlarval stages, to reach approximately 35% (d.w.), peaking to 50%, in adults (Fig. 3.26).

Figures 3.27 and 3.28 list lipid content in both percent and absolute values in relation to dry weight. Regression lines from the three areas, January and February Vestkapp Boxes and Filchner Depression, severally, accord with power functions that are so similar, whether calculated from percentages or absolute values, that in Figures 3.27 and 3.28 only the resultant from all data has been drawn in. Percent total lipid rises, at first steeply together with dry weight, from low levels during the young stages, then plateaus around 40-45%, having reached "saturation" (Fig. 3.27).

Figures 3.29 and 3.30 describe the relationship between lipid classes (in mg or % d.w.) and total lipid weight/lipid content. Much as in E. superba, phosphatidylethanolamine remains nearly constant, while phosphatidylcholine, and even more wax esters, increase linearily with rising lipid weight/lipid content. The relation between the lipid classes (in mg) and dry weight (Fig. 3.31) resembles their relation

to lipid weight: while the quantity of phosphatidylethanolamine hardly increases, the weights of phosphatidylcholine and wax esters clearly rise with increasing dry weight.

Phospholipids (as % total lipid) of larval and postlarval stages (10-18 mm; Fig. 3.26) are identical (41.1%); these polar lipids decrease in the adult to 33.7-35.6%. There is an inverse relation between phospholipids and wax esters (as % total lipid). Whereas phospholipids decrease to a minimum of 35% with increasing lipid content, the wax esters rise steeply to a maximum of about 60%. Reduction in the percentage of phospholipids is due mainly to reduction of phosphatidylethanolamine, while there is a slight increase in the percentage of phosphatidylcholine in comparison to that of larvae. During the ontogeny of E. crystallorophias there is clear decrease in triglycerides from 20.6% to about 5%, together with an increase in wax esters from 27.2% to nearly 50%. Whereas storage lipid consists of triglycerides in E. superba, it is made up of wax esters in E. crystallorophias. Both species, in addition, accumulate large amounts of phosphatidylcholine.

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[For Tables and Figures translated below, see following intercalated pages]

Table 3.11. Station and Measurement Data of E. crystallophorias larvae (calyptopis I, furcilia I) and postlarvae, according to d.w.; Weddell Sea 1985 (53)

Table 3.12. Station and Measurement Data of E. crystallophorias (subadult and adult), according to d.w.; Vestkapp Box 1, Weddell Sea 1985 (54)

Table 3.13. Station and Measurement Data of E. crystallorophias (subadult, adult) according to d.w.; Vahsel Bay/Gould Bay, Weddell Sea 1985 (55)

Table 3.14. Station and Measurement Data of E crystallorophias (subadult, adult) according to d.w.; Vestkapp Box 2, Weddell Sea 1985

Figure 3.26. Lipid Content and Composition of E. crystallorophias (C: Jan. Box, D: Vahsel/Gould Bay, E: Feb. Box (56)

Figure 3.27. Lipid Content/Dry Weight Correlation in Euphausia crystallorophias (x: Jan. Box, +: Vahsel/Gould Bay, *: Feb. Box; log-log regression

Figure 3.28. Lipid/Dry Weight Correlation in Euphausia crystallorophias (o: larvae and postlarvae), x: Jan. Box, +: Vahsel/Gould Bay, *: Feb. Box; log-log regression (57)

Figure 3.29. Lipid Class/Total Lipid Weights in Euphausia crystallorophias; wax esters +; phosphatidylcholine o; phosphatidylethanolamine *; linear regression

Figure 3.30. Lipid Class (%d.w.)/Lipid Content in Euphausia crystallorophias; wax esters +; phosphatidylcholine o; phosphatidylethanolamine *; linear regression (58)

Figure 3.31. Lipid Class Weight/Dry Weight in Euphausia crystallorophias; wax esters +; phosphatidylcholine o; phosphatidylethanolamine *: linear regression

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Thysanoessa macrura G.O. SARS, 1883 (59)

Lipid data concerning Thysanoessa macrura from the environs of the Antarctic Peninsula and the Weddell Sea are presented in Tables 3.15-

Tab. 3.11. Stationsdaten und Messergebnisse von E. crystallorophias-Larven (Calyptopis I-Furciliae I) und Postlarven, nach Trockengewicht sortiert; Weddell See 1985

Stat. No.	Date D/M/Y	Haul Depth (m)	Stage/ Length (mm)	Total Number (n)	Mean WetWt (g)	Mean DryWt (g)	Mean Lipid (g)	Total Lipid %WetWt	Total Lipid %DryWt	Lipid Class Composition in Percent of Total Lipid: Polar	Neutral	PE	PS+ PI	PC	SM	LPC	WE+ SE	TAG	FFA	CHOL	DAG
307	08/02/85	230-0	C1,2i,3	200	0.00053	0.000064	0.000009	1.7	13.7	42.6	57.4	11.3	0.3	30.7	0.1	0.1	30.9	18.2	1.1	6.2	1.0
309	09/02/85	220-0	C1,2i,3	200	0.00056	0.000067	0.000007	1.2	10.3	43.0	57.0	12.7	0.5	29.5	0.1	0.1	22.3	19.5	4.1	7.9	3.3
258	24/01/85	227-0	C2+3	120	0.00092	0.000101	0.000012	1.4	12.3	38.4	61.6	8.4	0.4	28.9	0.3	0.3	27.8	18.1	5.0	6.9	3.9
269	26/01/85	210-0	C2+3	200	0.00095	0.000116	0.000014	1.5	12.5	45.0	55.0	10.0	0.3	34.3	0.2	0.2	24.3	18.4	1.8	7.2	3.2
315	12/02/85	190-0	C3	200	0.00107	0.000134	0.000020	1.9	14.9	43.6	56.4	11.5	0.3	31.6	0.1	0.2	23.7	22.3	0.8	6.5	3.0
336	16/02/85	180-0	C3	36	0.00119	0.000136	0.000030	2.5	21.8	28.2	71.8	6.2	0.0	21.4	0.3	0.3	37.4	26.8	1.4	4.9	1.4
315	12/02/85	190-0	F1	200	0.00195	0.000264	0.000039	2.0	14.7	43.7	56.3	8.6	0.1	34.8	0.1	0.1	26.6	21.3	2.1	6.3	0.0
336	16/02/85	180-0	F1	123	0.00203	0.000270	0.000042	2.1	15.6	44.0	56.0	10.5	0.3	33.2	0.0	0.1	24.3	20.2	2.0	6.6	2.9
Mean								1.8	14.5	41.1	58.9	9.9	0.3	30.5	0.2	0.2	27.2	20.6	2.3	6.6	2.3
Std.Dev.								0.4	3.4	5.6	5.6	2.1	0.2	4.3	0.1	0.1	5.0	2.9	1.5	1.5	1.4
309	09/02/85	220-0	11-13	125	0.0114	0.00146	0.00022	1.9	15.2	37.9	62.1	6.0	0.2	30.9	0.3	0.4	38.1	12.1	3.0	5.7	3.3
275	29/01/85	195-0	12-15	19	0.0176	0.00243	0.00043	2.5	17.9	39.9	60.1	4.9	0.8	33.4	0.3	0.4	36.2	10.0	4.6	6.1	3.3
296	04/02/85	215-0	12-15	6	0.0162	0.00245	0.00063	3.9	25.8	40.4	59.6	4.5	0.0	35.8	0.0	0.1	42.4	10.3	2.6	4.3	0.0
307	08/02/85	230-0	12-15	75	0.0183	0.00249	0.00055	3.0	22.1	43.0	57.0	5.4	0.0	37.2	0.2	0.2	41.0	8.7	1.9	4.6	0.8
292	04/02/85	225-0	10-15	27	0.0162	0.00287	0.00065	4.0	22.6	42.3	57.6	5.7	0.0	35.9	0.3	0.4	43.7	6.6	2.3	5.0	0.0
290	02/02/85	225-0	10-15	56	0.0223	0.00327	0.00069	3.1	21.2	42.8	57.2	5.6	0.0	37.0	0.1	0.2	44.6	5.9	1.7	5.0	0.0
302	06/02/85	220-0	15-18	50	0.0274	0.00399	0.00096	3.5	24.0	41.6	58.4	4.7	0.0	36.6	0.2	0.2	46.6	7.3	0.0	4.6	0.0
302	06/02/85	220-0	15-18	49	0.0316	0.00457	0.00114	3.6	24.9	41.9	58.1	3.5	0.0	38.2	0.1	0.1	43.2	8.1	2.5	4.2	0.0
307	08/02/85	230-0	15-18	27	0.0347	0.00593	0.00171	4.9	28.9	40.3	59.7	3.6	0.1	36.2	0.2	0.2	47.1	6.5	2.0	4.0	0.0
309	09/02/85	220-0	16-18	3	0.0478	0.00732	0.00176	3.7	24.1	41.0	59.0	4.5	0.1	35.6	0.4	0.4	43.3	8.5	2.3	4.1	0.7
Mean								3.4	22.7	41.1	58.9	4.8	0.1	35.7	0.2	0.3	42.6	8.4	2.3	4.8	0.8
Std.Dev.								0.8	3.9	1.6	1.6	0.9	0.2	2.1	0.1	0.1	3.4	2.0	1.1	1.1	1.3

Tab. 3.12. Stationsdaten und Messergebnisse von E. crystallorophias (subadult und adult), nach Trockengewicht sortiert; Vestkapp Box 1, Weddell See 1985

Stat. No.	Date D/M/Y	Haul Depth (m)	Total Number (n)	Approx. Length (mm)	Mean WetWt (g)	Mean DryWt (g)	Mean Lipid (g)	Total Lipid %WetWt	Total Lipid %DryWt	Lipid Class Composition in Percent of Total Lipid: Polar	Neutral	PE	PS+ PI	PC	SM	LPC	WE+ SE	TAG	FFA	CHOL	DAG
271	27/01/85	190-0	1	20	0.0526	0.0109	0.0034	6.4	30.9	38.6	61.3	4.4	0.1	33.9	0.0	0.2	49.0	3.5	4.3	4.0	0.7
275	29/01/85	195-0	2	20	0.0796	0.0164	0.0052	6.6	31.9	38.1	61.9	2.7	0.0	35.4	0.0	0.0	47.6	5.7	2.6	4.2	1.9
282	30/01/85	200-100	1	22	0.0800	0.0170	0.0063	7.9	36.9												
282	30/01/85	200-100	1	23	0.0887	0.0181	0.0050	5.7	27.9	40.6	59.4	4.3	0.3	35.3	0.3	0.4	39.4	8.1	4.9	4.4	2.5
282	30/01/85	200-100	1	24	0.0967	0.0221	0.0080	8.3	36.3	38.8	61.2	2.0	0.3	36.2	0.1	0.2	48.2	5.8	2.2	3.1	1.9
271	27/01/85	190-0	1	25	0.1087	0.0232	0.0068	6.2	29.2	38.5	61.5	3.4	0.2	34.8	0.0	0.1	45.0	5.6	4.7	3.7	2.3
282	30/01/85	200-100	1	26	0.1105	0.0244	0.0088	8.0	36.2												
282	30/01/85	200-100	1	25	0.1091	0.0248	0.0093	8.5	37.5												
271	27/01/85	190-0	1	28	0.1440	0.0290	0.0080	5.5	27.5	39.7	60.3	3.1	0.6	35.9	0.0	0.1	46.4	3.1	4.3	4.5	1.9
271	27/01/85	190-0	1	26	0.1514	0.0313	0.0122	8.1	39.1												
282	30/01/85	200-100	1	28	0.1563	0.0324	0.0115	7.3	35.4												
282	30/01/85	200-100	1	27	0.1519	0.0339	0.0128	8.4	37.7	36.3	63.6	1.7	0.0	34.4	0.0	0.3	55.0	3.2	2.1	3.4	0.0
271	27/01/85	190-0	1	27	0.1566	0.0378	0.0143	9.1	37.9	37.1	62.9	2.2	0.3	34.6	0.0	0.0	48.0	6.1	4.4	3.4	0.9
271	27/01/85	190-0	1	29	0.1981	0.0449	0.0143	7.2	31.8	36.2	63.8	2.3	0.0	33.6	0.2	0.2	49.9	5.0	3.8	4.0	1.1
271	27/01/85	190-0	1	30	0.2048	0.0487	0.0187	9.1	38.4												
282	30/01/85	200-100	1	30	0.2217	0.0502	0.0191	8.6	38.0												
282	30/01/85	200-100	1	31	0.2075	0.0502	0.0203	9.8	40.3	36.3	63.7	1.2	0.0	35.0	0.0	0.1	51.3	4.4	5.2	2.7	0.0
271	27/01/85	190-0	1	33	0.2524	0.0517	0.0165	6.5	31.8	40.6	59.4	2.1	0.0	38.3	0.1	0.2	49.5	3.9	2.7	3.3	0.0
282	30/01/85	200-100	1	31	0.2116	0.0531	0.0207	9.8	39.0												
282	30/01/85	200-100	1	32	0.2480	0.0581	0.0228	9.2	39.3	34.7	65.3	1.2	0.0	33.4	0.0	0.2	53.0	4.0	2.6	3.6	2.1
282	30/01/85	200-100	1	32	0.2480	0.0631	0.0264	10.6	41.8	36.7	63.3	1.2	0.1	35.3	0.0	0.1	50.8	6.0	2.9	2.8	0.9
282	30/01/85	200-100	1	37	0.3861	0.0938	0.0350	9.1	37.3	36.7	63.3	1.4	0.0	35.0	0.1	0.1	54.0	4.3	2.1	2.9	0.0
Mean								8.0	35.6	37.8	62.2	2.4	0.1	35.1	0.1	0.2	49.1	4.9	3.5	3.6	1.2
Std.Dev.								1.4	4.1	1.8	1.8	1.1	0.2	1.2	0.1	0.1	4.0	1.4	1.1	1.1	0.9

Tab. 3.13. Stationsdaten und Messergebnisse von E. crystallorophias (subadult, adult), nach Trockengewicht sortiert; Vahsel Bucht/Gould Bay, Weddell See 1985

Stat. No.	Date D/M/Y	Haul Depth (m)	Total Number (n)	Approx. Length (mm)	Mean WetWt (g)	Mean DryWt (g)	Mean Lipid (g)	Total Lipid %WetWt	Total Lipid %DryWt	Lipid Class Composition in Percent of Total Lipid: Polar	Neutral	PE	PS+ PI	PC	SM	LPC	WE+ SE	TAG	FFA	CHOL	DAG
309	09/02/85	220-0	1	28	0.1293	0.0172	0.0015	1.2	8.9	58.6	41.4	23.5	2.2	31.4	1.3	0.3	14.0	7.0	3.2	17.2	0.0
307	08/02/85	230-0	1	24	0.0833	0.0218	0.0095	11.4	43.6	37.6	62.4	1.7	0.0	35.8	0.0	0.1	52.1	6.0	1.6	1.8	0.9
292	04/02/85	225-0	1	27	0.1191	0.0292	0.0120	10.1	41.0	36.3	63.7	2.1	0.0	34.0	0.1	0.2	55.7	3.9	1.4	2.6	0.0
302	06/02/85	220-0	1	25	0.1357	0.0300	0.0123	9.1	41.1	37.2	62.8	2.4	0.0	34.3	0.2	0.3	51.7	3.5	3.2	2.2	2.1

Tab. 3.13. Stationsdaten und Messergebnisse von E. crystallorophias (subadult, adult), nach Trockengewicht sortiert; Vahsel Bucht/Gould Bay, Weddell See 1985

Stat. No.	Date D/M/Y	Haul Depth (m)	Total Number (n)	Approx. Length (mm)	Mean WetWt (g)	Mean DryWt (g)	Mean Lipid (g)	Total Lipid %WetWt	Total Lipid %DryWt	Lipid Class Composition in Percent of Total Lipid												
										Po-lar	Neu-tral	PE	PS+ PI	PC	SM	LPC	WE+ SE	TAG	FFA	CHOL	DAG
309	09/02/85	220-0	1	28	0.1293	0.0172	0.0015	1.2	8.9	58.6	41.4	23.5	2.2	31.4	1.3	0.3	14.0	7.0	3.2	17.2	0.0
307	08/02/85	230-0	1	24	0.0833	0.0218	0.0095	11.4	43.6	37.6	62.4	1.7	0.0	35.8	0.0	0.1	52.1	6.0	1.6	1.8	0.9
292	04/02/85	225-0	1	27	0.1191	0.0292	0.0120	10.1	41.0	36.3	63.7	2.1	0.0	34.0	0.1	0.2	55.7	3.9	1.4	2.6	0.0
302	06/02/85	220-0	1	25	0.1357	0.0300	0.0123	9.1	41.1	37.2	62.8	2.4	0.0	34.3	0.2	0.3	51.7	3.5	3.2	2.2	2.1
292	04/02/85	225-0	1	30	0.1891	0.0359	0.0064	3.4	17.8	44.3	55.7	7.4	0.3	36.2	0.3	0.2	34.9	10.2	4.3	5.2	1.1
302	06/02/85	220-0	1	28	0.1557	0.0362	0.0152	9.7	41.8												
302	06/02/85	220-0	1	29	0.2086	0.0393	0.0130	6.2	33.2	35.9	64.1	1.9	0.0	34.0	0.0	0.0	49.4	7.6	2.4	3.3	1.3
302	06/02/85	220-0	1	33	0.2380	0.0468	0.0140	5.9	30.0	39.7	60.3	2.9	0.0	36.4	0.2	0.2	47.2	6.1	2.2	2.6	2.2
292	04/02/85	225-0	1	34	0.2531	0.0535	0.0136	5.4	25.5	39.5	60.5	3.2	0.2	35.6	0.2	0.3	46.1	5.9	3.9	4.6	0.0
292	04/02/85	225-0	1	37	0.3483	0.0703	0.0215	6.2	30.5	35.3	64.7	1.9	0.0	33.2	0.2	0.0	56.1	2.5	1.9	4.2	0.0
302	06/02/85	220-0	1	35	0.3257	0.0735	0.0291	8.9	39.6	38.7	61.3	1.4	0.0	37.0	0.1	0.2	47.5	5.6	3.3	2.2	2.5
299	05/02/85	240-0	1	34	0.2655	0.0822	0.0411	15.5	50.0	37.5	62.5	1.3	0.0	36.0	0.0	0.2	50.4	5.0	2.9	1.8	2.5
299	05/02/85	240-0	1	38	0.4125	0.0916	0.0272	6.6	29.7	38.5	61.5	2.4	0.0	35.9	0.1	0.1	51.3	3.6	1.4	3.3	1.8
302	06/02/85	220-0	1	39	0.4900	0.1188	0.0573	11.7	48.2	36.8	63.2	0.8	0.0	36.0	0.0	0.0	58.7	2.1	0.5	1.1	0.7
302	06/02/85	220-0	1	40	0.5362	0.1280	0.0546	10.2	42.7	35.4	64.6	1.2	0.0	34.2	0.0	0.0	53.4	5.3	1.8	2.0	2.2
299	05/02/85	240-0	1	38	0.4574	0.1314	0.0610	13.3	46.4	36.6	63.4	1.1	0.0	35.5	0.0	0.0	54.4	3.5	2.3	1.5	1.8
Mean								8.4	35.6	39.2	60.8	3.7	0.2	35.0	0.2	0.1	48.2	5.2	2.4	3.7	1.3
Std.Dev.								3.7	11.4	5.8	5.8	5.7	0.6	1.5	0.3	0.1	11.0	2.1	1.0	1.0	1.0

Tab. 3.14. Stationsdaten und Messergebnisse von E. crystallorophias (subadult, adult), nach Trockengewicht sortiert; Vestkapp Box 2, Weddell See 1985

Stat. No.	Date D/M/Y	Haul Depth (m)	Total Number (n)	Approx. Length (mm)	Mean WetWt (g)	Mean DryWt (g)	Mean Lipid (g)	Total Lipid %WetWt	Total Lipid %DryWt	Lipid Class Composition in Percent of Total Lipid												
										Po-lar	Neu-tral	PE	PS+ PI	PC	SM	LPC	WE+ SE	TAG	FFA	CHOL	DAG
319	13/02/85	385-200	4	18-21	0.0551	0.0101	0.0019	3.5	19.0	47.7	52.2	8.3	0.2	38.8	0.2	0.2	38.1	3.6	3.7	5.7	1.2
358	24/02/85	180-0	1	20	0.0607	0.0129	0.0047	7.7	36.3	36.5	63.5	4.2	0.7	31.1	0.3	0.2	42.9	9.1	4.2	4.7	2.6
315	12/02/85	50-0	1	20	0.0576	0.0133	0.0050	8.7	37.7	38.9	61.1	2.5	0.0	36.3	0.0	0.1	46.3	6.0	4.4	3.8	0.7
319	13/02/85	200-20	1	25	0.1031	0.0223	0.0062	6.0	27.8	41.5	58.5	4.8	0.5	35.9	0.2	0.2	37.3	10.0	3.8	4.5	2.8
319	13/02/85	385-200	3	25-28	0.1286	0.0269	0.0078	6.1	29.0	40.9	59.1	2.3	0.5	37.8	0.2	0.2	47.3	4.2	2.5	4.1	1.0
358	24/02/85	180-0	1	26	0.1211	0.0304	0.0121	10.0	39.8	36.3	63.7	1.9	0.0	33.9	0.2	0.2	54.7	4.2	1.8	2.4	0.6
358	24/02/85	180-0	1	25	0.1297	0.0327	0.0135	10.4	41.2	36.9	63.1	1.6	0.5	34.8	0.0	0.0	50.7	5.8	3.5	3.1	0.0
358	24/02/85	180-0	1	27	0.1687	0.0390	0.0150	8.9	38.5	35.6	64.4	1.5	0.1	33.8	0.1	0.1	52.1	5.9	2.7	3.7	0.0
319	13/02/85	385-200	1	30	0.1997	0.0422	0.0142	7.1	33.7	38.2	61.8	2.1	0.0	35.8	0.1	0.1	51.0	4.1	2.6	3.5	0.6
358	24/02/85	180-0	1	28	0.1809	0.0448	0.0170	9.4	37.9	35.9	64.1	1.9	0.0	33.5	0.2	0.3	50.7	4.9	3.5	2.6	2.4
358	24/02/85	180-0	1	33	0.2581	0.0593	0.0177	6.8	29.7	39.0	61.0	2.0	0.6	36.0	0.2	0.2	46.5	4.8	3.5	4.5	1.7
Mean								7.7	33.7	38.9	61.1	3.0	0.3	35.2	0.2	0.2	47.1	5.7	3.3	3.9	1.2
Std.Dev.								2.0	6.7	3.5	3.6	2.0	0.3	2.1	0.1	0.1	5.7	2.1	0.8	0.8	1.0

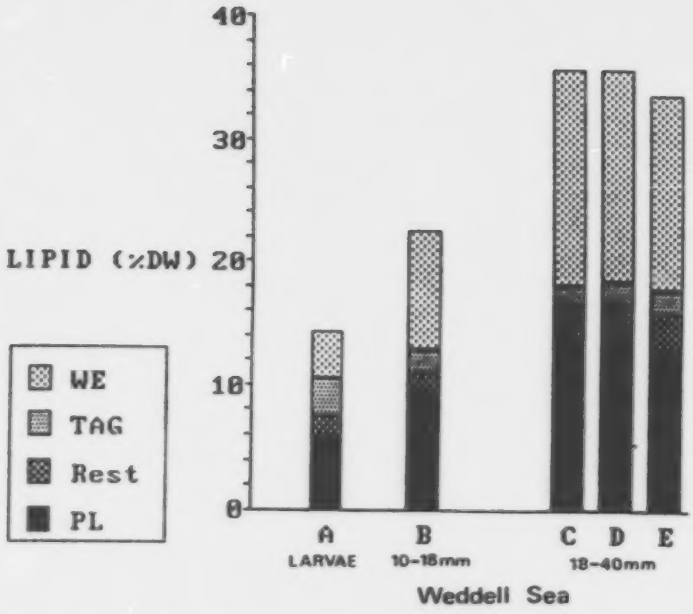


Abb. 3.26. Lipidgehalt und -zusammensetzung von *Euphausia crystallorophias* (C: Jan.-Box, D: Vahsel/Gould Bay, E: Feb.-Box)

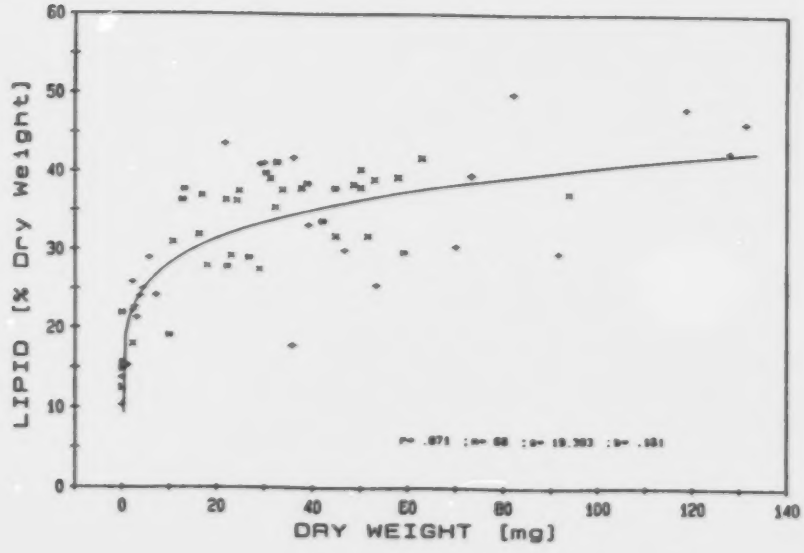


Abb. 3.27. Lipidgehalts-/Trockengewichtsbeziehung von *Euphausia crystallorophias* (x: Jan.-Box, +: Vahsel/Gould Bay, *: Feb.-Box; doppelt logarithmische Regression)

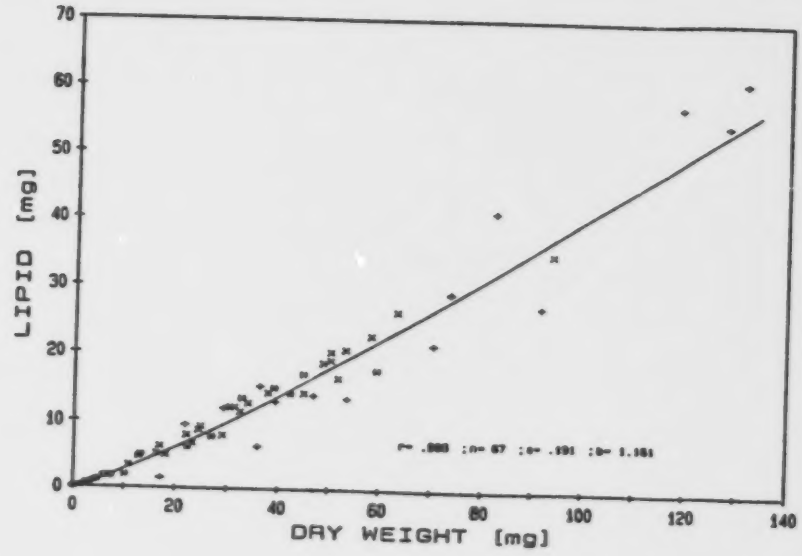


Abb. 3.28. Lipid-/Trockengewichtsbeziehung von *Euphausia crystallorophias* (o: Larven und Postlarven, x: Jan.-Box, +: Vahsel/Gould Bay, *: Feb.-Box; doppelt logarithmische Regression)

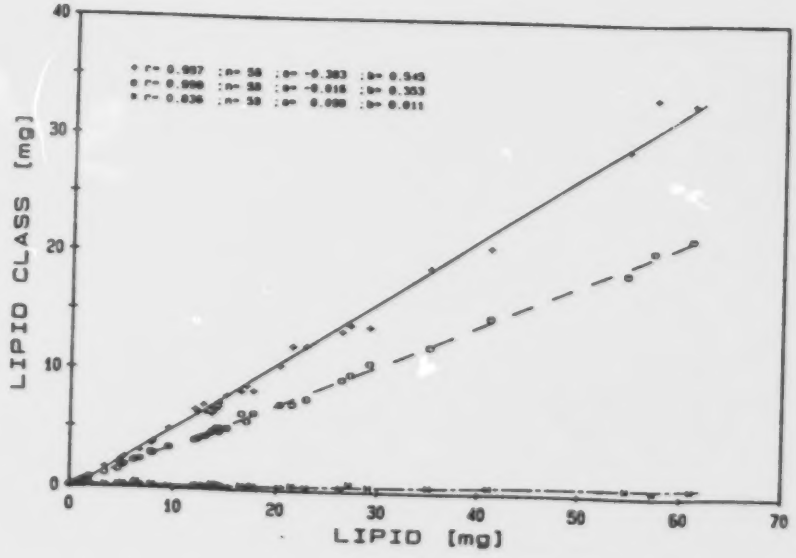


Abb. 3.29. Lipidklassengewicht/Gesamtlipidgewicht von *Euphausia crystallorophias*; Wachsester +; Phosphatidylcholin o; Phosphatidylethanolamin *; lineare Regression

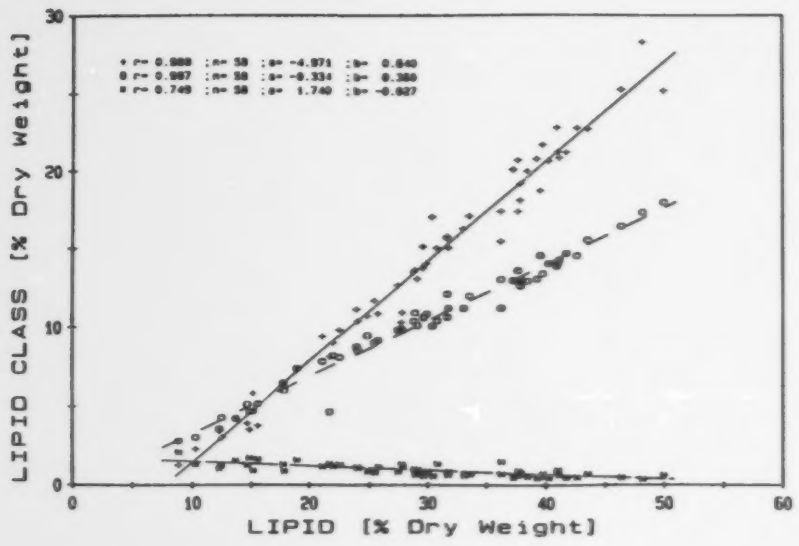


Abb. 3.30. Lipidklassen (% TG)/Lipidgehalt von *Euphausia crystallorophias*; Wachsester +; Phosphatidylcholin o; Phosphatidylethanolamin *; lineare Regression

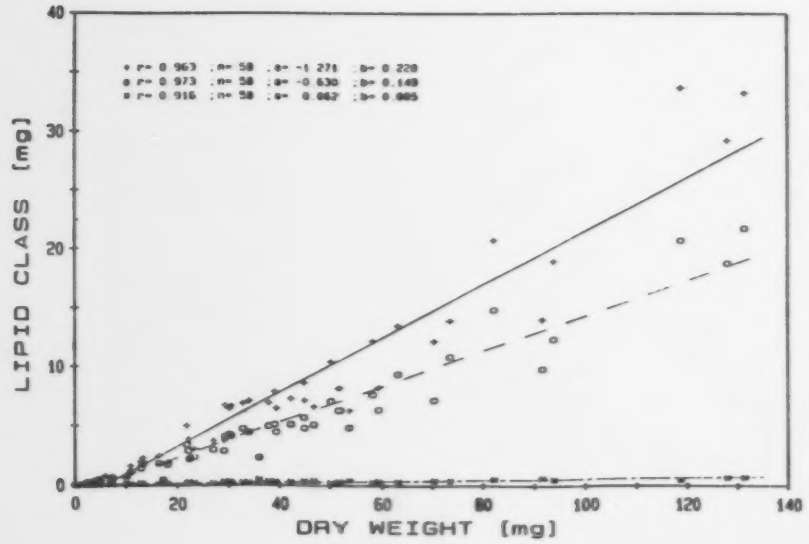


Abb. 3.31. Lipidklassengewicht/Trockengewicht von *Euphausia crystallorophias*; Wachsester +; Phosphatidylcholin o; Phosphatidylethanolamin *; lineare Regression

3.17 and Figures 3.32-3.35. October/November data from animals measuring 11-20 mm in length show a low lipid content of about 10% together with low dry weight (Fig. 3.32). This level has increased in animals caught in January 1985 (15-24 mm) to 29.5%, but in those from the Weddell Sea (11-27 mm), collected mainly in February, it averaged 37.4% of dry weight. The percentage of total lipids in animals caught near the Antarctic Peninsula in October/November 1983 and in January 1985 showed little variation, whereas differences were large, between the extremes of 19% and 47%, in the Weddell Sea (Vestkapp Box). Th. macrura furcilia I and II (Tab. 3.16, Fig. 3.32) caught in the February Box off Vestkapp contain -- as do those of the juvenile stages of the other two euphausid species -- little lipid (13.9%), but during maturation this increases rapidly to about 40% of dry weight.

Figure 3.33 also shows increases of lipids correlated to dry weight for the various months and regions.

Correlation between lipid classes (in mg or % d.w.) and total lipid weight/content is given in Figures 3.34 and 3.35. As in the two other euphausid species, phosphatidylethanolamine hardly varies with lipid weight (Fig. 3.34), and decreases only a little when calculated in relation to lipid content (Fig. 3.35). In opposition to this, phosphatidylcholine and, even more, wax esters clearly increase linearily with rising lipid content.

As already noted for the other two euphausid species, the phospholipid fraction, as % of total lipid, decreases to about 35% as lipid content increases. Simultaneously, the wax ester fraction rises to above 60%. Thus, in October/November animals from the Antarctic Peninsula the phospholipid fraction (48.6%) is distinctly higher than in specimens caught in January (39%). Remarkably, the phosphatidylcholine fraction still is on the increase in January animals, while phosphatidylethanolamine drops precipitously, from 16.8% to 1.9%. The situation is similar for animals from the Weddell Sea. Reduction of the percentage of phosphatidylethanolamine with rising total lipid content appears to be a general phenomenon among antarctic Euphausiaceae. Opposed to this, phosphatidylcholine (% dry weight) increases linearily with increasing lipid content, which suggests that this lipid has a storage function in the three species investigated.

Sterol percentages have also dropped sharply in the January/February animals (13.2%-3.8%/3.4%). For neutral lipds, higher lipid content is due to a rise of wax esters from 24.7% to 55.5%/56.2% (Fig. 3.32). Adult Th. macrura contain virtually no triglycerides, but the free fatty acid fraction (8.5%) is relatively high in the lipid-poor October/November 1983 specimens. It is possible that free fatty acids appear, as percentages, more prominent because of low absolute lipid quantities. Hardly any free fatty acids were demonstrable in Th. macrura taken in January off the Antarctic Peninsula and in February in the Weddell Sea.

[For Tables and Figures translated below, see following intercalated pages]

Table 3.15. Station and Measurement Data of Thysanoessa macrura, according to d. w.; Antarctic Peninsula October/November 1983 and January 1985 (60)

Table 3.16. Station and Measurement Data of Thysanoessa macrura (furcilia I and II) Vestkapp Box 2, Weddell Sea 1985 (61)

Table 3.17. Station and Measurement Data of Thysanoessa macrura (subadult, adult), according to dry weight; Vestkapp Boxes 1 and 2, Weddell Sea 1985

Figure 3.32. Lipid Content and Composition of Thysanoessa macrura (A: 11-20 mm; B: 15-24 mm; C: furcilia I,II; D: 11-27 mm) (62)

Figure 3.33. Lipid-/Dry Weight Correlation in Thysanoessa macrura (+: Oct./Nov. 1983, Antarctic Peninsula, linear regression; *: Jan. 1985 Antarctic Peninsula, linear regression; o: Jan./Feb. 1985, Weddell Sea, log-log regression

Figure 3.34. Lipid Class/Total Lipid Weights in Thysanoessa macrura (Antarctic Peninsula, Weddell Sea): wax esters +; phosphatidylcholine o; phosphatidylethanolamine *; linear regression (63)

Figure 3.35. Lipid Class (% d.w.)/Lipid Content in Thysanoessa macrura (Antarctic Peninsula, Weddell Sea): wax esters +; phosphatidylcholine o; phosphatidylethanolamine *; linear regression

Tab. 3.15. Stationsdaten und Messergebnisse von Th. macrura, nach Trockengewicht sortiert; Antarktische Halbinsel Oktober/November 1983 und Januar 1985

Stat. No.	Date D/M/Y	Haul Depth (m)	Total Number (n)	Approx. Length (mm)	Mean WetWt (g)	Mean DryWt (g)	Mean Lipid (g)	Total Lipid %WetWt	Total Lipid %DryWt	Lipid Class Composition in Percent of Total Lipid: Polar	Neutral	PE	PS+PL	PC	SH	LPC	WE	TAG	FFA	CHOL	DAG
156	05/11/83	200-0	10	11-16	0.0173	0.0028	0.00031	1.8	11.1	49.2	50.8	19.9	1.1	26.7	0.8	0.7	25.2	4.0	8.2	10.6	2.7
188	08/11/83	195-0	36	15-20	0.0191	0.0032	0.00030	1.6	9.3	50.5	49.5	17.8	0.3	31.2	0.8	0.5	19.3	3.1	9.1	15.5	2.5
156	05/11/83	200-0	10	13-17	0.0233	0.0037	0.00040	1.7	10.8	45.8	54.3	17.1	0.4	27.2	0.7	0.3	28.4	3.6	8.3	11.3	2.7
156	05/11/83	200-0	10	14-18	0.0257	0.0041	0.00036	1.4	8.8	49.6	50.4	18.5	0.9	28.4	1.0	0.7	17.2	4.7	10.6	14.7	3.2
102	24/10/83	200-0	40	<20	0.0246	0.0049	0.00054	2.2	11.1	47.9	52.1	14.2	0.0	32.9	0.5	0.3	30.2	3.6	6.1	12.3	0.0
156	05/11/83	200-0	10	16-20	0.0365	0.0060	0.00053	1.4	8.8	48.8	51.2	16.7	0.3	30.7	0.7	0.3	19.9	1.7	11.3	15.9	2.4
102	24/10/83	200-0	50	<20	0.0337	0.0066	0.00070	2.1	10.5	48.2	51.8	13.3	0.0	34.2	0.3	0.4	32.9	1.1	6.1	12.3	0.0
Mean								1.7	10.0	48.6	51.4	16.8	0.4	30.2	0.7	0.5	24.7	3.1	8.5	13.2	1.9
Std.Dev.								0.3	1.0	1.5	1.5	2.3	0.4	2.9	0.2	0.2	6.1	1.3	2.0	2.1	1.3
238	11/01/85	200-0	11	15-24	0.0360	0.0090	0.00244	6.8	27.0	37.2	62.8	2.4	0.0	34.6	0.2	0.0	57.4	1.4	0.0	4.0	0.0
238	11/01/85	200-0	10	17-20	0.0444	0.0118	0.00336	7.6	28.4	38.7	61.3	2.3	0.0	36.1	0.3	0.0	56.0	1.5	0.0	3.9	0.0
238	11/01/85	200-0	10	17-21	0.0501	0.0134	0.00407	8.1	30.3	40.7	59.3	1.9	0.0	38.7	0.1	0.0	52.4	2.1	0.0	4.0	0.8
238	11/01/85	200-0	10	17-22	0.0558	0.0146	0.00458	8.2	31.3	39.0	61.0	1.4	0.0	37.5	0.1	0.0	55.4	1.8	0.0	3.8	0.0
238	11/01/85	200-0	10	21-22	0.0607	0.0157	0.00477	7.9	30.4	39.4	60.6	1.6	0.0	37.7	0.1	0.0	56.5	0.7	0.0	3.4	0.0
Mean								7.7	29.5	39.0	61.0	1.9	0.0	36.9	0.2	0.0	55.5	1.5	0.0	3.8	0.2
Std.Dev.								0.6	1.8	1.3	1.3	0.4	0.0	1.6	0.1	0.0	1.9	0.5	0.0	0.2	0.4

Tab. 3.16. Stationsdaten und Messergebnisse von Thysanoessa macrura (Furcilien 1 und 2); Vestkapp Box 2, Weddell See 1985

Stat. No.	Date D/M/Y	Haul Depth (m)	Total Number (n)	Mean WetWt (g)	Mean DryWt (g)	Mean Lipid (g)	Total Lipid %WetWt	Total Lipid %DryWt	Lipid Class Composition in Percent of Total Lipid											
									Po-lar	Neu-tral	PE	PS+ PI	PC	SM	LPC	WE+ SE	TAG	FFA	CHOL	DAG
315	12/02/85	190-0	200	0.00075	0.00010	0.000014	1.9	13.9	47.1	52.9	11.8	0.7	34.1	0.3	0.2	24.8	16.5	0.0	8.5	3.1

Tab. 3.17. Stationsdaten und Messergebnisse von Thysanoessa macrura (subedult, adult), nach Trockengewicht sortiert; Vestkapp Box 1 und 2, Weddell See 1985

Stat. No.	Date D/M/Y	Haul Depth (m)	Total Number (n)	Approx. Length (mm)	Mean WetWt (g)	Mean DryWt (g)	Mean Lipid (g)	Total Lipid %WetWt	Total Lipid %DryWt	Lipid Class Composition in Percent of Total Lipid											
										Po-lar	Neu-tral	PE	PS+ PI	PC	SM	LPC	WE+ SE	TAG	FFA	CHOL	DAG
271	27/01/85	190-0	2	11-12	0.0094	0.0019	0.0008	8.0	38.7	39.5	60.5	3.6	0.0	35.3	0.1	0.5	49.7	3.7	3.6	3.6	0.0
322	13/02/85	198-0	18	12-14	0.0131	0.0030	0.0010	7.5	33.2	37.6	62.4	2.0	0.0	35.5	0.1	0.0	56.3	1.9	0.0	3.3	0.9
271	27/01/85	190-0	2	14-16	0.0230	0.0040	0.0007	3.2	18.8	45.7	54.3	8.6	0.0	36.1	0.5	0.4	39.3	4.2	3.8	7.0	0.0
340	17/02/85	225-0	10	12	0.0376	0.0053	0.0018	4.8	33.8	37.2	62.8	1.3	0.0	35.6	0.1	0.1	57.3	2.2	0.0	2.6	0.6
337	16/02/85	220-0	1	15	0.0193	0.0059	0.0024	12.5	40.9	35.4	64.6	1.2	0.0	34.1	0.1	0.1	55.9	3.5	1.1	2.6	1.4
340	17/02/85	225-0	1	19	0.0429	0.0120	0.0055	12.8	46.1	35.8	64.1	0.7	0.0	35.1	0.1	0.1	59.8	1.7	0.0	2.6	0.0
271	27/01/85	190-0	6	20-21	0.0563	0.0132	0.0048	8.5	36.4	36.5	63.5	1.0	0.0	35.4	0.1	0.0	57.7	1.3	1.6	2.8	0.0
340	17/02/85	225-0	1	20	0.0606	0.0173	0.0078	12.9	45.1	34.0	66.0	0.9	0.0	33.0	0.1	0.0	60.9	2.3	0.0	2.8	0.0
319	13/02/85	385-200	7	15-20	0.0674	0.0180	0.0078	11.6	43.3	33.2	66.8	0.6	0.0	32.7	0.0	0.0	61.1	2.5	0.0	3.2	0.0
340	17/02/85	225-0	1	23	0.0700	0.0190	0.0073	10.4	38.5	36.9	63.1	0.9	0.0	35.8	0.1	0.1	57.0	2.2	1.2	2.2	0.4
324	14/02/85	205-0	1	22	0.0810	0.0196	0.0078	9.7	40.0	36.5	63.5	0.7	0.0	35.8	0.0	0.0	57.8	1.3	0.6	2.6	1.1
340	17/02/85	225-0	1	22	0.0753	0.0207	0.0097	12.9	47.1	33.5	66.5	0.5	0.0	33.0	0.1	0.0	57.8	2.4	1.1	3.3	1.9
337	16/02/85	205-0	1	25	0.0902	0.0234	0.0088	9.7	37.6	36.8	63.2	1.1	0.0	35.5	0.2	0.1	56.4	1.5	0.5	3.6	1.2
319	13/02/85	385-200	1	25	0.1001	0.0244	0.0084	8.4	34.4	34.5	65.5	1.6	0.0	32.7	0.2	0.0	57.8	2.6	1.5	3.6	0.0
328	14/02/85	190-0	1	27	0.1297	0.0279	0.0065	5.0	23.3	38.1	61.9	2.5	0.0	35.4	0.2	0.1	52.4	1.2	1.6	5.3	1.3
319	13/02/85	385-200	1	27	0.1746	0.0492	0.0204	11.7	41.5	32.8	67.2	0.6	0.0	31.9	0.1	0.0	62.4	1.5	0.0	3.2	0.0
Mean								9.4	37.4	36.5	63.5	1.7	0.0	34.6	0.1	0.1	56.2	2.3	1.0	3.4	0.6
Std.Dev.								3.1	7.7	3.1	3.1	2.0	0.0	1.4	0.1	0.1	5.5	0.9	1.2	1.2	0.7

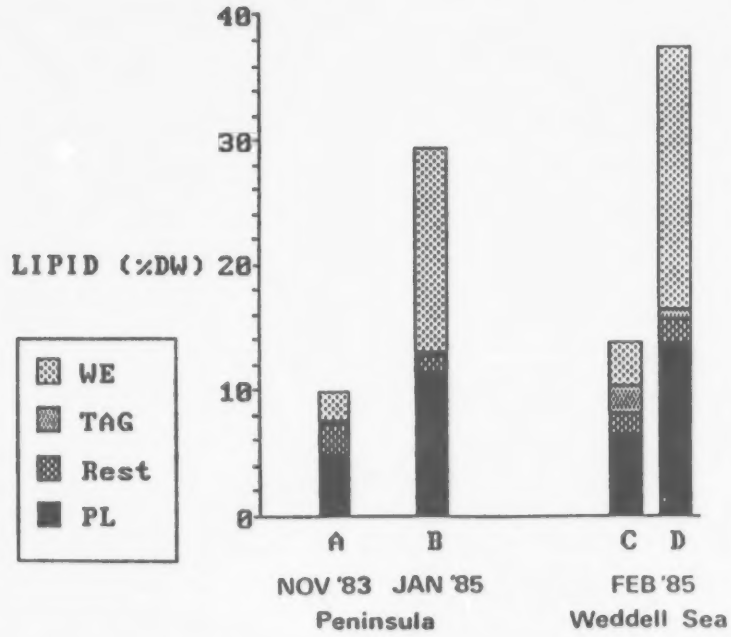


Abb. 3.32. Lipidgehalt und -zusammensetzung von *Thysanoessa macrura* (A: 11-20mm; B: 15-24mm; C: Furcilien 1 und 2; D: 11-27mm)

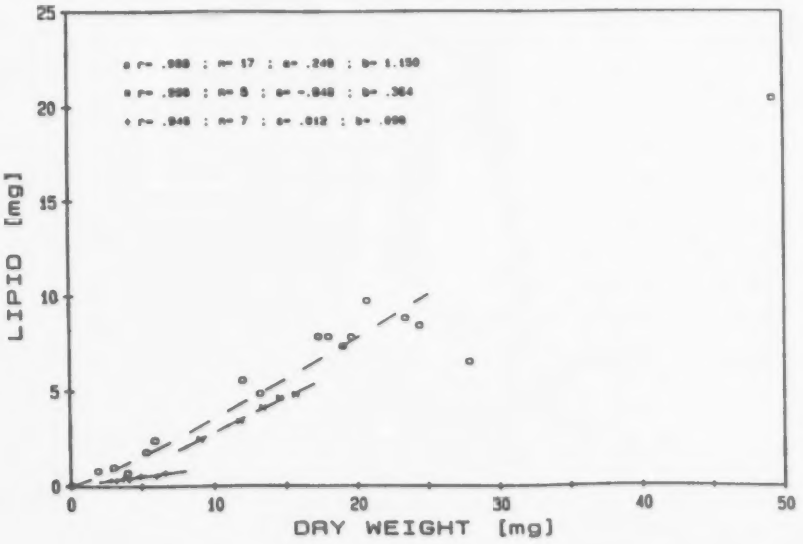


Abb. 3.33. Lipid-/Trockengewichtsbeziehung von *Thysanoessa macrura* (+: Okt./Nov. 1983, Antarktische Halbinsel, lineare Regression; *: Jan. 1985, Antarktische Halbinsel, lineare Regression; o: Jan./Feb. 1985, Weddellmeer, doppelt logarithmische Regression)

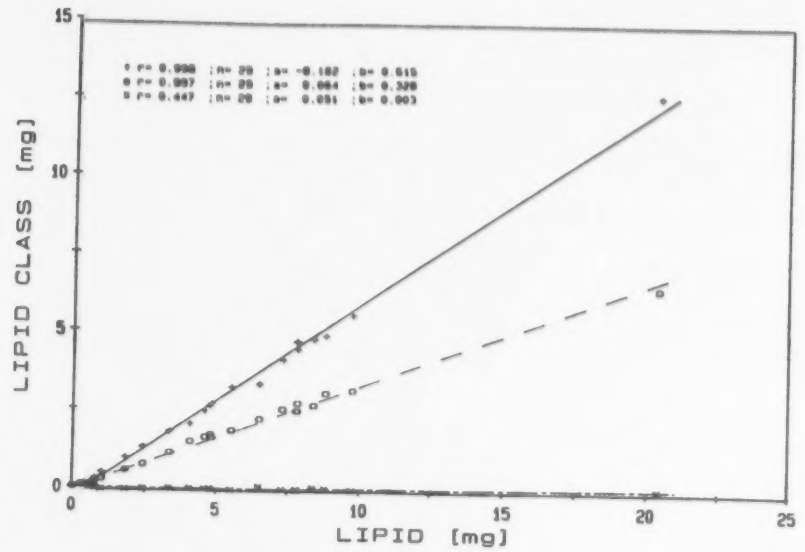


Abb. 3.34. Lipidklassengewicht/Gesamtlipidgewicht von *Thysanoessa macrura* (Antarktische Halbinsel, Weddellmeer): Wachsester +; Phosphatidylcholin o; Phosphatidylethanolamin x; lineare Regression

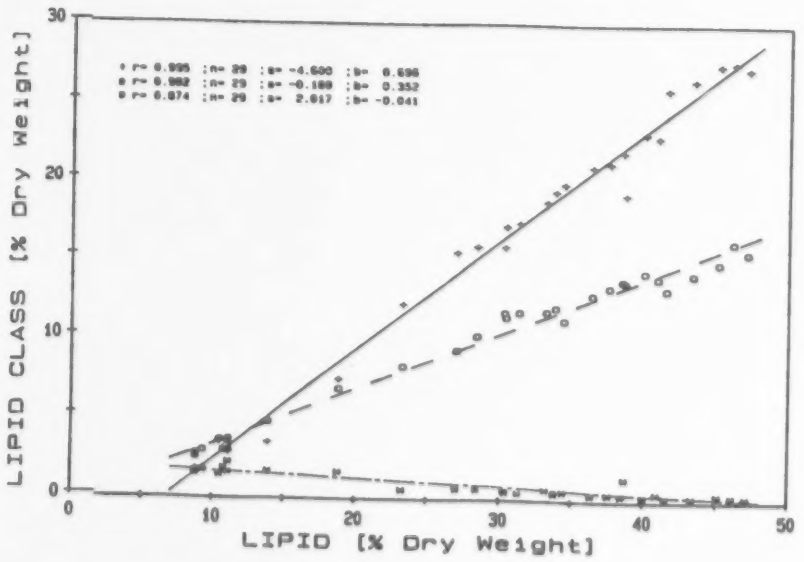


Abb. 3.35. Lipidklassen (% TG)/Lipidgehalt von *Thysanoessa macrura* (Antarktische Halbinsel, Weddellmeer): Wachsester +; Phosphatidylcholin o; Phosphatidylethanolamin x; lineare Regression

4. DISCUSSION (92)

4.1 Copepods

4.1.1 Ontogeny

At present, there are only a few studies that address lipid contents of the various developmental stages of copepods. In general, lipid studies have concerned themselves only with C V and adult stages. LEE et al. (1974) followed lipid changes throughout the entire developmental cycle of aquarium-held Euchaeta japonica. Similar laboratory studies are also extant for Calanus helgolandicus (probably C. pacificus), though these do not include all the developmental stages (LEE et al. 1972). KATTNER and KRAUSE (1987) analyzed ontogenic changes in the lipids of C. finmarchicus (C I to females, males) caught in their natural environment.

While Euchaeta eggs contain large amounts of wax esters, C. helgolandicus egg lipids are mainly triglycerides, but both species store primarily wax esters during development. Thus, female C. helgolandicus transform large amounts of triglycerides into wax esters during egg production. During the ontogeny of E. japonica, lipid levels continuously decrease from ovum, through nauplius to copepodid C II. According to LEE et al. (1974) C I emerge from the eggs of this species even without nutrient intake. It is not until C IV is reached (C III not reported) that there is a clear increase in lipid content. Highest lipid levels occurred in C V and mature females, whereas immature female E. japonica contained distinctly lower lipid contents. BAMSTEDT and MATTHEWS (1975) measured the lipid

contents of a subarctic species, Euchaeta norvegica (ova, C IV, C V, females, males). The general trend of their results agrees well with the results by LEE et al. (1974). KATTNER and KRAUSE (1987) found that lipids increased exponentially -- particularly wax esters -- in C. finmarchicus from C I to C V.

Our antarctic copepods were also studied as separate stages, particularly Calanus propinquus (C II, C III, C V, females, males) and Euchaeta antarctica (C III, C IV, C V, females, males). The tendency to accumulate lipids, starting from early copepodid stages to the adult, already noted by other investigators, was also apparent in these antarctic species. For example, lipid content of C. propinquus rises from 18% (d.w.) at C II to maximal levels of over 55% (d.w.) in C V and females. In Euchaeta antarctica, lipid content rises from 14% d.w. in the C IV to a maximum of 45% d.w. in C V and 40% d.w. in females. This increase in lipids during ontogeny is also apparent from studies of various developmental levels of Rhincalanus gigas, Metridia gerlachei and Calanoides acutus from the Weddell Sea. ANDREWS (1966) noted that in C. acutus advanced stages from C IV on, had large oil sacs, not found in C I to C III. This enrichment in lipids may be a general rule: at first, egg lipids furnish the energy necessary for growth and metabolism. As soon as the copepodids (or nauplii) start feeding, ever larger amounts of nutrients are stored as neutral lipids for overwintering and reproduction. Phospholipids barely increase. C V and mature females accumulate maximal amounts of lipids. When C V change into immature females, there is, at

first, a decline in lipid contents, just as in the antarctic species, C. acutus, C. propinquus, R. gigas and E. antarctica (see also LEE et al. 1974; SARGENT et al. 1977; KATTNER and KRAUSE 1987). GATTEN et al. (1980) found that in Calanus helgolandicus, a copepod from the temperate regions, half of the lipid content is catabolized during transformation into female and development of reproductive organs, (93)
while males loose hardly any lipids. After molting, the voraciously feeding females again acquire large amounts of lipids. Euchaeta japonica C V use the major fraction of their lipids for oogenesis. (LEE et al.. 1974). The increase in lipid content during ontogeny is caused by the large increase in storage lipids which, in C V and females, can account for over 90% of total lipids.

It is noteworthy that the lipid content of C. propinquus males is distinctly less than that of E. antarctica males. In both species the males resorb their mouth parts (MIZDALSKI pers. comm.; HOPKINS 1987). It is possible that C. propinquus males had discontinued feeding after their estival reproductive period, whereas reproduction for Euchata males does not take place until fall/winter (LITTLE-PAGE 1964). BAMSTEDT (1979) assesses the life span of males of Euchaeta norvegica to be no more than one month. According to HOPKINS et al. (1984b), the life span of C. finmarchicus males is approximately two months. In these males they found a clear diminution of dry weight and carbon content, and explain this loss of organic reserves by the increased physical activity during pairing (see also SARGENT and HENDERSON 1986).

All our observations make it quite clear that young copepodids are the sensitive stages in the life cycle of these copepods, and that it is especially important for these young stages to find sufficient food, as they do not have adequate reserves to outlive starvation. Subadults and adults, on the other hand, are known to survive long periods without food (e.g. LEE et al. 1972). BAMSTEDT and MATTHEWS (1975) found that lipid reserves accumulated by C V and females determined the success of the following generation.

Among copepodid stages -- and, in part, also among females -- of C acutus, C. propinquus, R. gigas, and E. antarctica there is, over a broad range, a highly significant correlation between dry weight and lipid weight. BAMSTEDT and MATTHEWS (1975) also found this true in E. norvegica. It should therefore be possible to estimate the lipid content of these species (Weddell Sea, summer) from their dry weight by use of a regression equation.

4.1.2 Storage Lipids

As a rule, phospholipids and cholesterol are structural elements of the plasma membrane, whereas triglycerides and wax esters are used in plankton as energy stores (LEE et al. 1970a,b; SARGENT 1976). But, at present there is no satisfying answer to why bathypelagic and polar marine copepods accumulate wax ester rather than triglyceride stores (CLARKE 1983). For herbivorous copepods this requires conversion of phytoplankton lipids -- the lipids of algae consist

primarily of triglycerides, with hardly any wax esters -- into wax esters (LEE et al. 1972; SARGENT 1976).

Various hypotheses have been put forth to explain the predominance of wax esters in copepods. LEE et al. (1971a) name, as factors possibly affecting lipid composition: environmental temperature, differential compressibility and molar volumes of the various lipid classes and regulatory activity of lipid catabolizing enzymes. LEE et al. (1971a,b) found that copepods first catabolize their triglycerides and then, but more slowly, their wax esters. From this, BENSON and LEE (1972, 1975) conclude that triglyceride catabolizing enzymes are constantly active, while those catabolizing wax esters only become active during periods of stress and starvation, so that wax ester stores can be preserved for times of duress. Furthermore, LEE et al. (1972) also consider constant vs. seasonal availability of food, and phylogenetic relations, as causes of differential lipid composition. (94)

The lack of wax esters in fresh water antarctic copepods (SARGENT 1976; see also CLARKE 1984a) contradict the view that environmental temperature may be the cause of major wax ester storage. These animals store triglycerides; the lake whence they were collected is ice-bound most of the year but has available minimal amounts of food (phytoplankton, detritus) throughout the year. This example seems to support the hypothesis of LEE and SARGENT that wax esters serve as long-term reserves to protect from the periods of starvation that occur primarily in bathyal or polar waters (LEE et al. 1971a; BENSON et al. 1972; SARGENT 1976, 1978; see also HAKANSON 1984).

According to SARGENT (1976, 1978) wax esters are best suited when large amounts of food (e.g. phyoplankton blooms) have to be stored with great rapidity in the form of lipids. Normally, de novo biosynthesis of lipids is blocked by enzymatic control mechanisms when large amounts of lipid are consumed. The advantage of wax ester synthesis (from long-chain alcohols and fatty acids) is that these inhibiting mechanisms are switched off, so that food proteins and carbohydrates can be transformed into wax esters, to add immediately to ingested lipids (SARGENT and McINTOSH 1974; SARGENT and HENDERSON 1986).

Current studies of polar sea copepods show that wax esters are the dominant class in lipid storage. They form the major part of storage lipids in the arctic species, Calanus glacialis, C. hyperboreus, C. finmarchicus, Pareuchaeta barbarata, Pareuchaeta glacialis, Euchaeta sp., Metridia longa, and in the antarctic species, Calanoides acutus, Rhincalanus gigas, Euchaeta antarctica, and Metridia gerlachei (LEE 1975; CLARKE 1984a; SARGENT and HENDERSON 1986; REINHARDT and VAN VLEET 1986). Exceptions from higher latitudes (British Columbia, North Sea) are the omnivorous species Eucalanus bungii (Temora longicornis), Acartia clausi, Centropages hamatus, which store primarily triglycerides (LEE 1974; KATTNER et al. 1981).

The clear predominance of the wax ester fraction among the lipids of the above named antarctic copepods is confirmed in our study. Only M. gerlachei has a significant fraction of triglycerides in addition to the dominant wax esters, but the species stores only little lipid.

The two newly studied species, Calanus propinquus and Euchirella rostromagna, deviate from the above scheme and are the first known polar sea copepods in which triglycerides form the main lipid stores. In C. propinquus, triglycerides can represent more than 90% of the lipids. In view of the fact that the ten previously analyzed Calanus species, from tropical, subtropical, boreal and polar regions, store predominantly wax esters (SARGENT and HENDERSON 1986) -- the only exception is the lipid-poor tropical species, C. minor (LEE and HIROTA 197[illegible] phylogenetic reasons can not be adduced to account for triglyceride accumulation in C. propinquus. On the basis of their Euphausiaceae data, SARGENT et al. (1981) claim that storage of triglycerides suggests year-round feeding (see Chap. 4.2.3). Whether the storage of triglycerides in C. propinquus means that this species occupies a different ecological niche than C. acutus and R gigas, and that, in contrast to the wax ester storing herbivores, it also feeds in winter, can not be answered on the basis of current knowledge. HOPKINS (1985, 1987), in his studies on nutrition, has found that at the end of the summer (February-April; Ross Sea, Antarctic Peninsula) (95) C. propinquus feeds mainly on phytoplankton and only occasionally on smaller zooplankton. He classes C. propinquus with the "generalists" of the Ross Sea as part of a cluster comprising, among others, M. gerlachei, E. antarctica and the older stages of C. acutus. Cluster analysis of the nutrient composition from the Antarctic Peninsula assembles C. propinquus, E. rostromagna, Pleuromamma, Salpa thompsoni, and Tomopteris carpenteri (C. acutus ceases to feed in March/April).

In Euchirella rostromagna, the second species for which there are no earlier lipid studies extant, triglycerides also form the major lipid stores. A series of Euchirella species from tropical and subtropical seas, however, has been studied by LEE and HIROTA (1973). In each of the species involved -- Euchirella brevis, E. galeata, E. pulchra, E. rostrata and two undetermined Euchirella sp. -- triglycerides clearly predominated over wax esters. Thus, it is possible that phylogenetic factors are responsible for triglyceride storage in the antarctic E. rostromagna (see also LEE et al. 1971a). HOPKINS (1985) classes E. rostromagna as an omnivore, feeding on diatoms, dinoflagellates, smaller crustaceans and other zooplankton. Further research will have to show whether the relatively low lipid content (25-30% d.w.) in February, together with triglyceride storage, are indications that E. rostromagna feeds in winter.

4.1.3 Seasonality

Both distributions and life cycles of the five copepod species under consideration here have been studied by many investigators (e.g. OTTESTAD 1932, 1936; MACKINTOSH 1934, 1937; OMMANNEY 1936; ANDREWS 1966). The dominant herbivorous species, Calanoides acutus, Calanus propinquus and Rhincalanus gigas were at the focus of interest. VORONINA (1972a,b) has described for these three species with similar nutritional requirements (SCHNACK 1985) a distribution pattern showing the temporal and spatial separation of their centres of distribution. This succession of the species prevents competition for food. According to VORONINA (1972b), in spring, when the ice retreats, the first

overwintering C IV and C V of C. acutus rise to the surface from greater depths (see also ANDREWS 1966). They go through a molt to the adult stage and lay their eggs in the epipelagic zone. After a period of intense feeding and growth the C IV, C V and females of C. acutus begin their journey into the depths. The overwintering stages of C. propinquus appear at the surface after C. acutus, spawn and feed, as the latter, on phytoplankton. R. gigas follows C. propinquus some time later, then goes through the same cycle. Mature females spawn and probably die, while C IV and C V copepodids migrate to the depths to overwinter. The further south the animals live, the later, and probably shorter, is the time these three species spend in the epipelagic zone. The spatial separation between the three species is therefore due to their different centres of distribution in terms of geographical latitude. Thus, R. gigas is more nearly a subantarctic species, which is predominantly found north of the Antarctic convergence (OMMANNEY 1936); it is rare in the high antarctic (BOYSEN-ENNEN 1987). C. acutus extends furthest to the south.

HOPKINS (1985) believes that the spring phytoplankton bloom in the Antarctic suffices to cover the energy requirements of herbivorous plankton. In fact, in the high Antarctic 95% of the phytoplankton biomass is said to remain unused by the zooplankton and to settle out (HOPKINS 1987). HOPKINS (1985) also believes that a carefully balanced, efficient exploitation of nutrients ("resource partitioning"), as considered by VORONINA (1972a,b), may thus be unnecessary in the Antarctic, and that C. acutus, C. propinquus and R. gigas, after fully exploiting primary production, greatly reduce or stop feeding in summer/fall.

MARIN (1986; in press a,b) believes with HOPKINS (1985) that because of plentiful primary production the three copepod species do not face any food competition. According to MARIN (1986; in press a,b) the life cycles of these species evolved independently. (96)

When one studies the lipid data of these copepods, one notes, first of all that C. acutus and R. gigas contain only small amounts of lipids, 17-23% and 6-9% of d.w., respectively, during the southern spring (early November) near the Antarctic Peninsula; the fraction of storage wax esters represents about 60-70% of the lipids in C. acutus and 50-60% in R. gigas. Body weight of the animals collected during the spring at the Peninsula was quite low compared to that of animals of the same stages collected in January/February from the Weddell Sea, suggesting that the feeding phase for the former had only just begun. The 1983/84 phytoplankton bloom was not well advanced at the time the samples were collected (NAST and GIESKES 1986), and did not reach its height until end December (VON BODUNGEN 1986). According to VORONINA's (1972a,b) scheme, C. acutus should have been the first species to reach the surface, which may explain its higher lipid content. The considerable quantities of wax esters in C. acutus, which is the first to spawn in the spring (see also OTTESTAD 1936) are used primarily for reproduction. GATTEN et al. (1980) discovered that in the boreal Calanus helgolandicus half the lipids are consumed during transition from C V to female, while much of the remaining lipids (wax esters) are used in spring for reproduction.

The other lipid data concerning C. acutus, C. propinquus and R. gigas were obtained in January/February (southern summer) from the southern Weddell Sea. This, therefore, represents a discontinuity within the season, and a geographic relocation from the Subantarctic to the High Antarctic. Here, the following picture emerges: the sub-adult stages and females of C. acutus have accumulated about 40-50% of d.w. as lipids, more than 90% of which are wax esters. Compared to species of the subantarctic this represents nearly a doubling of the lipid fraction, most of it from wax esters. Compared to January, the abundance of C V and female C. acutus at the surface is much reduced in February (HUBOLD et al. 1980). This suggests that these stages have ended their feeding cycle (SCHIEL, pers. comm.; see also HOPKINS 1985) even though enough phytoplankton is still available (VON BODUNGEN et al. 1988). Clearly, females disappear from the epipelagic zone after spawning, while the C V have replenished energy reserves in January/February and begin their journey into greater depths.

Similarly high, end-of-season (stages not given) lipid contents are reported by CLARKE (1984a), with 13% of wet weight (54% of this wax esters), and by REINHARDT and VAN VLEET 91986), with 45% of d.w., or 11% w.w. (64% wax esters). ANDREWS (1966) divides the oil sacs of the various developmental stages of C. acutus into four subjective categories (empty to full) and notes definite seasonal differences, with a maximum of lipids in May/June and a minimum at end of winter. According to ANDREWS (1966) the size of oil sacs in females varies less during the year than in C IV and C V. He assumes that these

stages do not feed in winter and that the lipids are used as reserve nutrient. The lipid data of the authors cited all originated from subantarctic regions (South Georgia, Antarctic Peninsula).

Obeying VORONINA's (1972a,b) concept C. propinquus goes through (97)
the same generational cycle as C. acutus, only with a time-lag. Can this timing shift be elucidated by the lipid data? In January, in the Wedell Sea, C V and females of C. propinquus have only average lipid contents of 26% and 25% d.w., but within two to three weeks, these values increase to 47% in C V, and 43% in females. These data suggest that, in January, C propinquus was still in the mid-feeding and stores-accumulating phase at a time when C. acutus already had extremely high lipid contents; C. propinquus does not reach that level until February. This is also supported by laboratoy experiments showing that C. propinquus has much higher feeding rate/unit weight ratios than C. acutus (SCHIEL pers. comm.). Thus, the concept of time-shifted cycles in C. acutus and C. propinquus postulated by VORONINA (1972a,b) finds support in that C. propinquus accumulates its lipids late. This suggests that the overwintering stages of C. propinquus actually do migrate into the epipelagic zone after those of C. acutus. They begin to utilize the primary product only after the needs of C. acutus have already been met.

The lowest lipid levels, 6-9% d.w., were found in the third herbivorous copepod, Rhincalanus gigas, during southern spring off the Antarctic Peninsula. In February, in the Weddell Sea, R. gigas is distinctly richer in lipids (C V, females) with 27-30% d.w., 85% of

which are wax esters. Compared to the two species discussed above, lipid content of R. gigas is distinctly lower in February, and there was no indication of significant lipid enrichment during the southern summer's collecting period. Lipid content of R. gigas in February corresponds approximately to that of C. propinquus in January. It is questionable, however, whether R. gigas, which, according to VORONINA (1972b), is the last of these three species to appear in the epipelagic zone, continues to increase lipid stores. In fact, for this subantarctic species the southern Weddell Sea represents the limit of its distribution and presumably offers unfavourable living conditions.

The few lipid data on R. gigas of the subantarctic (February/April), most without mention of stages (LEE and HIROTA 1973; CLARKE 1984a; REINHARDT and VAN VLEET 1986), are extremely heterogeneous (lipid contents 8-69% d.w.; wax ester fraction 50-92%) but do show that R. gigas is able to store much greater quantities of lipids than those measured in the Weddell Sea.

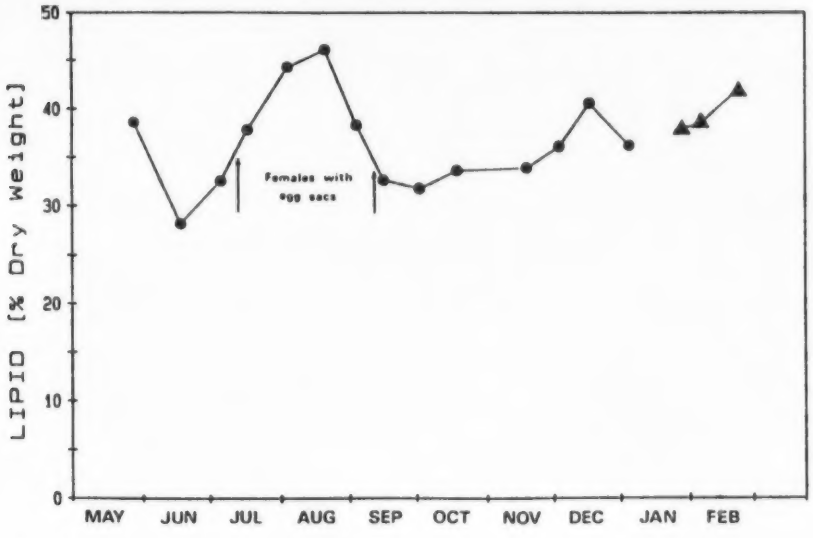
In opposition to the above discussed herbivorous copepods, Metridia gerlachei is omnivorous (SCHNACK 1983; HOPKINS 1987). There was little lipid accumulation (from 16% to 20% d.w.) by females in the Weddell Sea during January/February; the wax ester fraction increased from 30% up to 52%. For the same species, REINHARDT and VAN VLEET (1986) found similar levels during March/April in a sample (no stage) taken off the Antarctic Peninsula (21% d.w., 52% wax esters). The observation that M. gerlachei does not accumulate much lipid reserve, contrary to the herbivorous species, suggests that, being a

nutritional opportunist (HOPKINS 1985), it finds adequate food even in winter. According to SCHNACK-SCHIEL (1987) M. gerlachei does not stop feeding when chlorophyll levels drop below a minimum of 10 µg/L, while C. acutus and C. propinquus both do.

The only copepod species in which lipid contents have been followed quantitatively nearly year-round is the mainly carnivorous #Euchaeta antarctica. LITTLEPAGE (1964) measured lipid content in Euchaeta antarctica females of McMurdo Sound (77°S) from end May to end January at about two-week intervals. He found, in this species, at all times high lipid levels (> 30% d.w.), which peaked to 46% d.w. during gonad- and ovogenesis in July/August. Unfortunately, ice conditions prevented sampling at the end of the summer. That is why, in Figure 4.1, LITTLEPAGE's (1964) data from the Ross Sea have been supplemented by our summer (Weddell Sea) data of Euchaeta antarctica females (37-42% d.w.), which support the high lipid levels found in this species by LITTLEPAGE (1964). According to LITTLEPAGE, furthermore, lipid contents slowly increase after their fall during spawning. Our own data suggest -- with great reservations concerning the comparability of data -- that this trend is prolonged. CLARKE (1984a) also found very high lipid contents in Euchaeta females collected in mid-April off South Georgia. (98)

Figure 4.1. Seasonal Variation of Lipid Content in Euchaeta antarctica females:

● Data of LITTLEPAGE (1964) from Ross Sea
▼ Author's data from Weddell Sea; adapted from LITTLEPAGE (1964)



The question why carnivorous copepods need to accumulate such large lipid reserves is difficult to answer (see also CLARKE 1983). At present, it is not possible to determine whether lipids are used as energy reserves during overwintering at depth (VERVOORT 1965), or whether these animals also feed on plankton in winter. According to BAMSTEDT (1979) the subarctic Euchaeta norvegica consumes its lipid reserves over the winter because, at that time, the number of prey (copepods) drastically diminishes. LITTLEPAGE's (1964) data do not show any reduction of lipid stores during winter in E. antarctica. Euchaeta japonica can starve more than three months at 15°C without showing any diminution of its lipid stores (SARGENT 1978). The data of LITTLEPAGE (1964) reveal the importance of lipids for development

of gonads and ova in the female. But males also have lipid contents of approximately 40% d.w., even though their mouth parts are reduced after sexual maturation (HOPKINS 1987). It is possible that these lipids assist in buoyancy, but LITTLEPAGE (1964) argues that it is (99)
plankton from the low-viscosity tropical and temperate waters which would need high lipid levels for buoyancy. But as this is not the case, as in fact polar plankton has higher lipid levels, he considers lipids of little importance to buoyancy. Individuals of Euchaeta antarctica are much larger, however, than the other copepods and have a massive chitinous armour, so that without some means of flotation they would have to expend much swimming energy in order not to sink.

SUMMARY AND CONCLUSIONS:

The copepods under review, in particular the herbivorous species, compensate for the marked seasonality of primary productivity of the antarctic pelagic zone by, sometimes extraordinary, accumulations of lipid. Lipid stores serve as energy reserves and buoyancy aids. They insure that the copepods survive the nutrient-poor winter and are able to reproduce. As yolk reserves are essentially consumed during early ontogeny, survival of the first feeding stages depends on their finding an adequate nutritional environment quickly. During spring/summer, copepodids and adults accumulate -- in part, according to a species-specific schedule -- wax esters; two species primarily store triglycerides. So far, the reason for storing triglycerides rather than wax esters remains unclear.

4.2 Euphausiaceae

4.2.1 Ontogeny

Even though survival rate of larval stages has a major impact on the population density of antarctic krill (ROSS and QUETIN 1986), only a few studies focus on the physiology and biochemistry of the early stages of development. Lipid data are equally incomplete. CLARKE (1980) finds that the lipds of *E. superba* eggs weigh 9.3-9.6 µg; O'LEARY AMSLER and GEORGE (1985) find 9.4 µg, and estimate the lipid content of freshly spawned ova -- largest of Euphausiaceae eggs (MAUCHLINE and FISHER 1969) -- at 31% d.w.. By gastrulation (35 h after spawning) lipid content of the eggs has fallen to 28% d.w., and at the next stage (76 h after spawning; "limb bud stage") to 20% d.w.. While the eggs, which were spawned close to the surface, sink to greater depths (MARR 1962), the embryo has thus consumed a large amount of its lipids (38% of the starting level), but much protein (36%) is also catabolized. Five to eight days after the spawn, the nauplius larvae emerge and start their migration back to the surface ("developmental ascent", MARR 1962). After 13-25 days they reach the metanauplius-, after 30-34 days, the first calyptopis stage (e.g. MAUCHLINE 1980; IKEDA 1984a; MARSCHALL and HIRCHE 1984). This is the first feeding stage (MARSCHALL 1985). Our analyses (2,400 specimens) show that lipid contents in the first calyptopis had declined in mid-February in the Weddell Sea to an average of 11.6% d.w. (10.3-12.0%) during the energy consuming migration to the surface.

ROSS and QUETIN (1986) calculate, on the basis of the egg's energy content and the metabolic demands on the young larva, that the calyptopis I of E. superba should be able to starve for 6-12 days without deleterious effects on growth. In laboratory studies, they showed that a delay in feeding the first calyptopis retards larval development. Calyptopis I can survive nearly three weeks without food (lipid and protein catabolism), but then die within a few days; animals that are fed, on the other hand, progress through a molt to the calyptopis II stage. After 10-14 days of starvation, the animals (100) reach the "point of no return", and no longer molt nor progress to become calyptopis II. Food deprivation experiments (IKEDA 1984a) show that calyptopis I, starved for six days, cease their swimming movements. In the ocean, such organisms would sink back into the depths where there is no food and would starve to death. Our own calculations, following IKEDA and DIXON (1982), are derived from calyptopis lipid analyses and IKEDA's (1984b) respiration rates for calyptopis, which have the highest weight-specific oxygen consumption of all the developmental stages. These calculations show that, assuming all lipid reserves are burned up, the maximal life span of calyptopis I would be 5-10 days. This time-span would be even shorter if one took into account the absolutely vital plasma membranes; on the other hand, it is possible that proteins may also be catabolized. The permissible period of starvation estimated by ROSS and QUETIN (1986) thus corresponds closely to that calculated from lipid data of calyptopis I.

Thus, the calyptopis I is the critical stage, during which the energy reserves stored in the egg are mostly consumed. Within a month after hatching, larvae must reach a nutritionally favourable environment; if not, irreversible damage and larval death ensues. This short length of time stands in stark contrast to the long starvation periods (seven months) which IKEDA and DIXON (1982) found in juvenile and adult krill.

IKEDA (1984b) found that carbon content dropped from a maximum in the egg to a minimum in the calyptopis instars, after which the content rises again in furcilia, juveniles and adults. Nitrogen content hardly changes. He explains these results in terms of a rapid lipid decrease from ovum to calyptopis, followed by a rise of lipid content in the later stages (according to IKEDA 1984b, only 2% of the egg substance consists of carbohydrates).

According to our data, lipid content of actively feeding calyptopis II increases to 14.4% d.w. during February in the Weddell Sea, and the lipids consist of one third, each, phospholipids, triglycerides and wax or sterol esters. Thus, for the first time, there are now data (wet and dry weights, water content, lipid analyses) available to allow comparisons between calyptopis caught in the sea and those kept the laboratory.

Later development includes the third calyptopis and six furcilia stages. According to our data, late furcilia and juveniles caught in October/November (Antarctic Peninsula) display a low lipid content

(9-10% d.w.) after overwintering. Triglycerides are sparse; phospholipids and cholesterol predominate. Carbon and nitrogen analyses of furcilia show a C:N ratio of 4-5:1 (IKEDA 1984b), i.e. a body composition in which proteins predominate. Carbohydrates play only a minor role in marine zooplankton (e.g. RAYMONT and CONOVER 1961).

Ontogeny of juvenile, subadult and adult stages depends much on reproductive processes (gonadogenesis, spawning activities) and on seasonal factors (see Chapter 4.2.3). For instance, animals caught in October/November off the Antarctic Peninsula display a marked decrease in lipid content in relation to the dry weight of the animals. This may be because, when nutrition is inadequate, the energy required for metabolism increases with increasing body weight (KILS 1979; IKEDA 1984b; HEMPEL 1985b), so that larger animals consume their reserves more rapidly.

During January, off the Antarctic Peninsula -- at the height of the spawning season -- lipid contents are so variable that there is no significant correlation between lipid content and body weight. In January/February, in the Weddell Sea, on the other hand, lipid contents rise steeply from low levels in larvae (10-15% d.w.) to high values (25-30% d.w.) in larger animals. FERGUSON and RAYMONT (1974) also find a positive correlation between lipid content and body weight. Presumably, young animals transform their food mainly into muscle tissue (protein) (EHRLICH 1974), whereas adults use their energy not only for growth but also for gonadogenesis and the accumulation of lipid reserves. Body weight is not the principal factor in (101)

lipid accumulation; seasonal and ontogenic or reproductive factors are (see Chap. 4.2.3).

The eggs of E. superba sink to considerable depths (MARR 1962; HEMPEL and HEMPEL 1986), but those of the neritic E. crystallorophias remain suspended near the surface after they are spawned (MAKAROV 1979a; IKEDA 1986). It is not yet known whether the low density of these ova is due to a high lipid (wax esters ?) content (HARRINGTON and THOMAS 1987). IKEDA (1986) was able to keep spawned eggs of E. crystallorophias in the laboratory, where they developed over eight months into furcilia VI. The long time it took for development, and the high death rate, however, suggest that conditions in the holding tanks were less than adequate (insufficient food). In this paper, lipid measurements of the larval stages of E. crystallorophias (ferally caught) are presented for the first time. Just as in E. superba, mixed calyptopis I-III and II+III samples have low lipid contents, between 10% and 12.5% d.w.. By calyptopis III, lipid contents increase to 15% or 22% d.w.; lipid content of furcilia I are about 15% d.w.. In starving calyptopis, complete oxydation of their lipids would furnish energy sufficient for 9 to 18 days (estimate by IKEDA and DIXON 1982, on the basis of respiration rates measured in E. superba).

In E. crystallorophias, much as in E. superba from the Weddell Sea, lipid contents of the juvenile stages also quickly climb to about 23% d.w.. This accumulation of lipids continues in the adults, which have lipid contents of approximately 35% d.w.. There is, therefore,

a positive correlation between lipid content and body weight (lipid weight and body weight are unequivocally positively correlated). Phospholipids and wax esters predominate but triglycerides, contrary to the situation in E. superba, are insignificant except in the larvae.

The main spawning season of E. crystallorophias occurs during the southern spring (December), earlier than that of E. superba (e.g. HEMPEL et al. 1979; FEVOLDEN 1980), so that after the spawn, adults can replenish lipid reserves during the summer months. Such seasonal factors are discussed in Chap. 4.2.3. Overall, accumulation of lipid during the ontogeny of E. crystallorophias corresponds with that of Weddell Sea E. superba (except for differences between the various classes of neutral lipids).

The ova of Thysanoessa macrura, like those of E. superba, sink to greater depths, and their early stages go through "developmental ascent" (MAKAROV 1979b), as opposed to those of E. crystallorophias. Th. macrura begins spawning in September and its main spawning season is in November, earlier, therefore, as in either E. superba and E. crystallorophias (FEVOLDEN 1980; HEMPEL and HEMPEL 1982). This clearly reduces competition between the larvae of these species (MAKAROV 1979). At present, there are no laboratory studies of Th. macrura ontogeny. The furcilia I and II we analyzed had a low lipid content of 14% d.w., which approximates that of the first furcilia of E. E. crystallorophias (15% d.w.).

Much as in E. superba and E. crystallorophias, in Th. macrura lipid content of the larger animals in the Weddell Sea increases steeply, and, as in E. crystallorophias, phospholipids and wax esters predominate. At this time of year (late summer), a stage-dependent accumulation of lipids seems to be a general phenomenon shared by all the Euphausiaceae studied. The seasonal factors driving this lipid accumulation are discussed in Chap. 4.2.3. (102)

4.2.2 Storage Lipids

In the Euphausiaceae, contrary to the copepods, the high phospholipid content is noteworthy as it constitutes over one third of all lipids even in lipid-rich individuals (see also GRANTHAM 1977; BOTTINO 1974, 1975; CLARKE 1984a,b). Until recently, phospholipids were considered to be mainly structural elements of plasma membranes, but ELLINGSEN (1982) suggests that in the antarctic euphausid species, E. superba and in the arctic species Thysanoessa inermis and Th. raschi phospholipids are used as stores in addition to triglycerides and wax esters. He found in four analyses of E. superba a linear increase of triglycerides and phospholipids (each as % d.w.) with lipid content, but triglycerides increasing more than phospholipids. ELLINGSEN (1982) finds that in the subarctic species Meganyctiphanes norvegica, positive correlation occurs only between triglycerides and lipid content, while in the arctic Thysanoessa species triglycerides, wax esters and phospholipids all correlate positively with lipid content. From this, he concludes that these lipid classes, including phospholipids, are storage lipids, as phospholipids far exceed structural requirements.

In fact, in Thysanoessa and E. superba, they claim, biomembranes require an irreducible phosopholipid fraction of 3.5% d.w. fpr proper function (SAETHER et al. 1986).

ELLINGSEN'S (1982) hypothesis that in Euphausiaceae phospholipids serve as stores is supported by our extensive analyses, covering a wide range of lipid contents. This is reported here for the first time for the antarctic species E. crystallorophias and Th. macrura, in addition to E. superba, in which it has already been noted (ELLINGSEN and MOHR 1981). While E. superba deposits mainly triglycerides and little phospholipids with increasing lipid content, E. crystallorophias and Th. macrura accumulate primarily wax esters and phospholipids, only in much smaller amounts. Our investigations, in which we separated the various phospholipids, showed that only phosphatidylcholine (lecithin) was stored in significant amounts, while other phospholipids, such as phosphatidylethanolamine, had no importance as storage materials.

Why Euphausiaceae, contrary to other planktonic organisms, also store phosphatidylcholine (PC) is not clear; SAETHER et al. (1986) assume that PC storage can be explained by a need for its quick mobilization. It is also possible that the physical demands made on lipids by low antarctic temperatures may be connected to PC storage. It is knwon that phospholipids of antarctic plankton contain greater amounts of unsaturated fatty acids (CLARKE 1983) which, because of their greater fluidity, can maintain the proper function of biomembranes even at low temperatures. This hypothesis

is supported by the fact that no such PC accumulation was found in the subarctic species, M. norvegica. On the other hand, the other antarctic zooplankton survive without storing phospholipids. Maybe phosphatydilcholine is more easily stored in close vicinity to muscles and organs of Euphausiaceae, and so is immediately available when needed by these "high performance animals" (see KILS 1979), while triglycerides and wax esters have to be stored in concentrated form in (103)
depots in separate organs. Only more research will be able to explain why antarctic Euphausiaceae accumulate phosphatidylcholine.

The linear relationship between enrichment in lipid classes and lipid content can also be applied, in reverse, to lipid catabolism during starvation: as lipid content decreases, the various lipid classes, severally, decrease as functions of respective individual rates, triglycerides and wax esters in greater quantities than phospholipids. The hypothesis developed for other planktonic organisms, that during starvation selected classes of lipids are catabolized first, can thus not be demonstrated in Euphausiaceae (SAETHER et al. 1986).

Linear accumulation of storage lipids occurs in Euphausiaceae independently of sex, season or geographical origin, and apparently depends exclusively on the total lipid content. SAETHER et al. (1985) also show this linear correlation for different body fractions [Trans.: ? organs, body parts] of E. superba. The phenomenon thus seems to be based on a systemic process of accumulation. The independence from factors other than lipid content with which the various lipid classes,

severally, are accumulated, suggests the possibilty of assessing an organism's lipid class fractions from its lipid content. For this, one can use the known "accumulation regression lines" for each of the lipid classes of the three antarctic Euphausiaceae species as norms. The specific rates of accumulation (slope, intercept), in the three Euphausiaceae species studied here, much resemble one another, respectively, those of triglycerides and wax esters on the one hand, and those of phosphatidylcholine on the other.

4.2.3 Seasonality

So far, long-term seasonal lipid studies of antarctic Euphausiaceae exist only for Euphausia crystallorophias (LITTLEPAGE 1964). While there are many lipid analyses extant for Euphausia superba (see summary of MAUCHLINE and FISHER 1969; ELLINGSEN 1982; CLARKE 1980, 1984a,b), data for winter are missing, so that many questions about lipid enrichment of E. superba remain to be answered. Figure 4.2 summarizes the currently available data for total lipids in E. superba, insofar as they could be arranged in chronological order, and clearly shows the seasonal changes of lipid content between spring and fall. Interpretation of these data is complicated by their heterogeneity (geographic origin, size classes, sex, methodology). In spite of the great variability of the results, it is possible to follow the evolution of lipid contents, with their minimum in spring and maximum in fall (see also IKEDA and DIXON 1982; CLARKE 1984b). The lipid content of E. superba, however, never reaches the high levels seen in the other antarctic Euphausiaceae, E. crystallorophias

and Th. macrura. This reduced tendency to build stores, plus the fact that E. superba stores triglycerides -- instead of wax esters, as do E. crystallorophias and Th. macrura -- indicates to some authors (SARGENT 1976; SARGENT et al. 1981; CLARKE 1980, 1984b) that E. superba has access to food sources also in winter.

According to SARGENT and HENDERSON (1986), the hypothesis of LEE and HIROTA (1973) that wax ester accumulation in copepods is tied to wide seasonal fluctuations in nutrient availability, can now, in view of newer findings, also include the Euphausiaceae. From this SARGENT et al. (1981) postulate that E. crystallorophias (Antarctic) and Th. inermis (Arctic), two species that store primarily wax esters, are mainly herbivorous and only feed on small zooplankton and detritus in the fall, whereas Euphausia superba and Meganyctiphanes norvegica occupy different ecological niches. Because of the lack of wax esters, (104)
SARGENT et al. (1981) surmise that these triglyceride-storing species feed even in winter (see also CLARKE 1980, 1984b). According to their fatty acid spectra, M. norvegica feeds mainly on copepods, while E. superba eats primarily phytoplankton. The mainly carnivorous diet of M. norvegica has been confirmed by feeding studies (e.g. MAUCHLINE and FISHER 1969; KLAGES 1983). There is now also evidence that krill are phytophagous in winter.

Figure 4.2 Seasonal Variation of Total Lipid Content in Euphausia superba (spring-fall) according to published data.

(*) recalculated to % d.w., assuming 80% water content (CLARKE 1984b); in one-week intervals;

△♀♂ = literature data (subadults/mixed samples, females, males)
▲♀♂ = author's data (subadults without larvae/mixed samples, females, males)

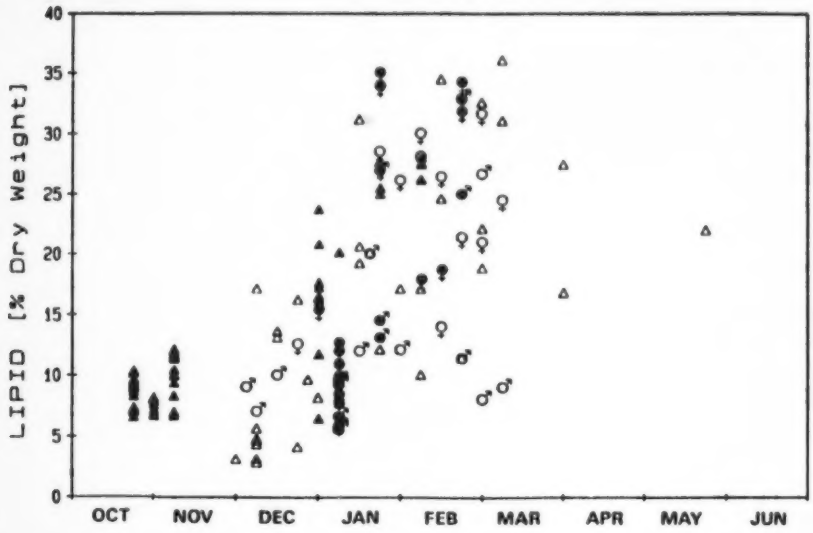


Abb. 4.2. Saisonale Veränderungen des Gesamtlipidgehalts von *Euphausia superba* (Frühling-Herbst): nach Literaturdaten von *KRYUCHKOVA & MAKAROV (1969), *MAUCHLINE & FISHER (1969), PIERCE *et al.* (1969), SIDHU *et al.* (1970), RAYMONT *et al.* (1971), FERGUSON & RAYMONT (1974), YANASE (1974), MORI & YASUDA (1976, in ELLINGSEN 1982), WATANABE *et al.* (1976), IWAYA *et al.* (1977, in ELLINGSEN 1982), ROSCHKE (1978), *CLARKE (1980), ELLINGSEN (1982), *FRICKE *et al.* (1984); * umgerechnet in Prozent

KAWAGUCHI et al. (1986) caught juvenile krill in winter in light traps on the bottom (40 m depth) of Lützow-Holm Bay (69°S). From May to August they recorded reduced metabolic rates in krill, which at that time apparently fed on detritus (prolonged sojourn of food in intestines). Beginning in August, when light intensity again rises, metabolic rates increase even though feeding conditions continue to be poor. Krill displays positive phototaxis. As light increases, ice algae begin to grow (see also HOLM-HANSEN and HUNTLEY 1984) and beginning in October the mid-gut (digestive) gland is no longer brownish (detritus) but green (KAWAGUCHI et al. 1986). In fact, KAWAGUCHI et al. (1986) assume, on the basis of carbon and nitrogen measurements, the in fall krill equally catabolises lipids as well as proteins, whereas in late winter it consumes mainly its lipid stores. (105)

This strategy for overwintering by feeding on detritus can be extrapolated to to the pelagic niche only with reservations. For this habitat we have observations by divers from the northern Weddell Sea that juvenile krill are found the year round in cracks in the pack-ice, and crop the algal lawn on the underside of the ice (KOTTMEIER and SULLIVAN, in press). The same phenomenon was seen also in adult krill during the "Polarstern" winter expedition of 1986, and photographed under-water by MARSCHALL (1987). The latter could show in the laboratory the great efficiency with which these animals use their filter-baskets to scrape algae off the under-side of the ice. But if krill finds adequate food in winter, this raises the question why it stores lipids in late summer.

The increased lipid content could serve for better buoyancy by the relatively heavy krill (KILS 1979); on the other hand, the krill could also use floes within the caves of the pack-ice as supports, so that there would be no difficulty in preventing sinking.

It is difficult to estimate the degree to which gonadogenesis affects lipid reserves. In E. superba, spawning can extend from mid-November to April, with a peak around January/February (ew.g. FRASER 1936; MAUCHLINE and FISCHER 1969; SIEGEL 1986). MAKAROV (1979a) and ROSS and QUETIN (1986) have suggested that krill spawns repeatedly in spring and summer (see also HARRINGTON and IKEDA 1986). SIEGEL (1986) has discovered that between March/April and October/November there is no shift in the relative frequencies of the developmental stages. The ova of krill examined by BARGMANN (1945) had reached measurable

size (< 0.1 mm) in August, but did not clearly enlarge (0.15 mm) until November. BARGMANN (1945) estimates that eggs need four months to ripen. This suggests that gonadogenesis takes place mainly during the of phytoplankton bloom, and that winter lipid reserves are not used for reproduction. ROSS and QUETIN (1986) calculated the energy necessary for the development of ovaries and found that the concentration of phytoplankton normally present in the pelagic regions of Antarctica are insufficient (see also HOLM-HANSEN and HUNTLEY 1984; HEMPEL 1985c). They conclude from this that krill only reproduce before the summer phytoplankton bloom if they are living in highly productive coastal areas, or can profit from ice-algae blooms in pack-ice. The authors do not take lipid reserves into consideration and believe that reproduction in krill is controlled mainly by the availability of food.

According to IKEDA and DIXON (1982), E. superba can survive long periods of starvation (211 days) by reducing metabolism and lessening body weight through protein catabolism. According to their figures, the lipid reserves of E. superba would last only 95 days at normal metabolic rates. They find that the chemical composition (carbon, nitrogen and phosphorus contents) of starving animals resembles that of animals taken in the wild, and conclude therefrom that lipids are not reduced during starvation; their results, however, are more likely to mean that all organic components are equally reduced. The strategy suggested by IKEDA and DIXON (1982) is highly unusual for plankton organisms from polar regions.

As we now know, however, E. superba is not forced to hunger permanently, and the fact that lipid contents become reduced during winter (see Fig. 4.2) suggest that lipid reserves in krill might serve as buffers in times of hunger. At present it is believed that growth of E. superba -- except, maybe, of late larval stages and juveniles (CHEKUNOVA and RYNKOVA 1974; SIEGEL 1986) -- is, at least, greatly slowed in winter (e.g BARGMANN 1945; EVERSON 1977; STEPNIK 1982; ROSENBERG et al. 1986). From this one may conclude that winter in spite of the ice-algae, is oligotrophic in comparison to summer. This may be related to the spotty distribution of algae; it may also be that algal availability is poorer in mid-winter than in spring. Little is known so far about the nutritional value of ice-algae. Studies of enzyme activity in E. superba (MUMM 1987) suggest that krill do not greatly reduce their metabolism in winter, nor go into a resting phase similar to the diapause of copepods (HIRCHE 1983). (106)

One must, however, discuss the question whether krill studies now extant have not led to false ideas concerning seasonal distribution patterns of E. superba. The lipid-poor animals that we caught far from the ice fields in October/November in Bransfield Strait may have drifted there, and may also have used up much of their lipid reserves in nutritionally poor waters before the start of the phytoplankton bloom (VON BODUNGEN 1986). On the other hand, it is possible that the "cryopelagic krill" in pack-ice has more lipids because of the more advantageous food situation. Whether, therefore, overwintering is associated with a noticeable reduction of lipid reserves, or

whether krill near ice does not use up its lipid stores because of better nutritional conditions, will have to be determined by analyses of the specimens collected last winter, which have not yet been processed. So far there are no convincing data supporting a slowing of krill growth in winter (CLARKE and MORRIS 1983). Should this phenomenon be confirmed, it would mean that, while ice algae and lipid reserves can maintain the basal metabolism of the animals, they do not provide the extra energy required for increasing biomass.

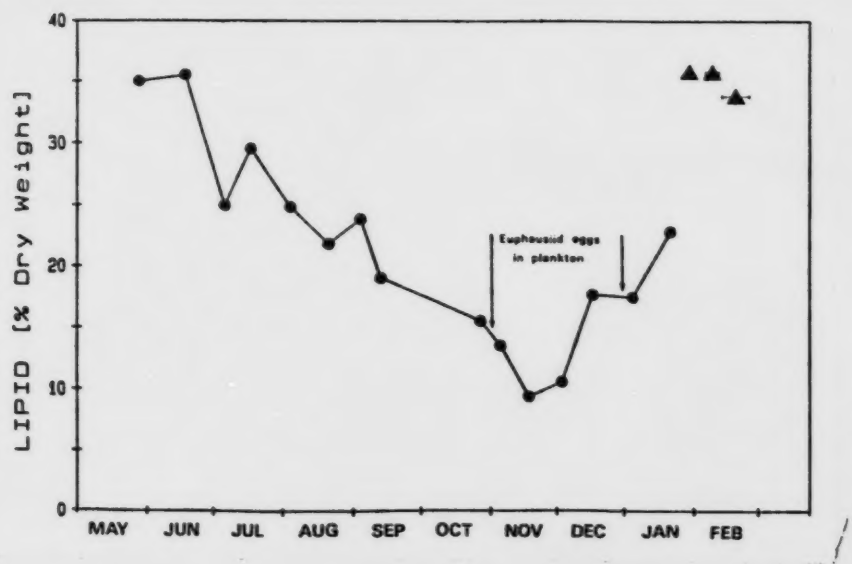
SIEGEL (1986) refers to the distribution pattern of krill during October/November as a winter condition. At that time, the hauls contained few krill, mostly juveniles and subadults (see also: NAST 1986). In South Georgia and off the Antarctic Peninsula, in winter, Chilean, English and German expeditions also found, either few, or no krill (GUZMAN 1983; HEYWOOD et al. 1985; SIEGEL 1987; see also: STEPNIK 1982), whereas in summer they are most widely distributed.

Considering the discoveries of SIEGEL (1986), the observations made during the winter expedition under the ice (KOTTMEIER and SULLIVAN in press; MARSCHALL 1987), and the present lipid data, seasonal lipid accumulation in krill together with the krill's distribution pattern can be summarized in an hypothesis, as follows: after the adults have spawned in the summer (formation of swarms) in ice-free pelagic waters (MAKAROV 1979a; QUETIN and ROSS 1984; SIEGEL 1985 a,b), they replenish their lipid reserves by feeding on phytoplankton; then, in fall, they retreat under the advancing ice. It is in the caves and clefts of the pack-ice that krill find both ice algae as winter food,

and protection from their predators (ANDRIASCHEV 1968; GUZMAN 1983; KOTTMEIER and SULLIVAN in press; MARSCHALL 1987). Thus, while adults move south after spawning, larval stages, after ascending from the depths, are disseminated by drift to the pelagic regions. This causes a spacial separation between the various developmental stages of the krill: the larvae that are ready to grow into furcilia stay in the vicinity of the edge of the pack-ice, whereas the actively migrating adults live in the more southerly regions, deeper in the ice (SIEGEL 1986). This separation of developmental stages is also confirmed by the observations of whalers: they regularly found small krill in the stomachs of blue whales, which feed at the edge of the pack-ice early in the season, and adult krill in the stomachs of fin-backs, which appear later in Antarctica (MARR 1962). This separation prevents competition between developmental stages and cannibalism of juveniles SIEGEL 1986). Only later larval stages and juveniles grow vigorously throughout winter (SIEGEL 1986). This may be explained by (107)
high productivity at the edge of the pack-ice. The less mature stages are also the first to profit from the intense phytoplankton bloom which occurs in spring in the vicinity of the pack-ice (SMITH and NELSON 1985, 1986). It is questionable whether individuals which fail to reach pack-ice in their migration and drift away, survive winter, though IKEDA and DIXON (1982) find that such animals can live seven months without food. At the beginning of spring, when pack-ice retreats, adult krill again undertake a spawning migration north into open waters, where they use a phytoplankton bloom to replenish their winter-depleted lipid stores and to initiate gonadogenesis. In summer, after mating, they then spawn in waters far from any coast.

The seasonal changes of lipid content in E. crystallorophias, a species from the High Antarctic, are well known (LITTLEPAGE 1964). The studies, conducted from end May to end January, reveal a constant decrease of lipid content from 35% d.w. in May to 10% d.w. in November. Thereafter, lipid content again increases slowly to 23% d.w. by end January, when LITTLEPAGE'S (1964) studies were concluded. A few of our data from February (Weddell Sea) suggest -- with reservations concerning their comparability -- a further increase of lipids to an average 35% d.w. by the end of summer, thus returning to the values found by LITTLEPAGE in May (Fig. 4.3). This species, which stores wax esters, therefore accumulates large amounts of lipid in spring/summer which the animals then use throughout the long High-Antarctic winter.

Figure: 4.3. Seasonal Changes of Total Lipid Content in Adult Euphausia crystallorophias: o Data from LITTLEPAGE (1964); ▲ author's means from Weddell Sea; adjusted from LITTLEPAGE (1964)



HOPKINS (1987), making nutritional studies during February in the Ross Sea, found that E. crystallorophias eats small zooplankton in addition to phytoplankton. As the organisms grow, their food shifts toward zooplankton. Stomach contents of E. crystallorophias taken in February in the relatively shallow Admirality Bay (South Shetland Islands) showed, in addition to plankton algae, a substantial fraction of benthic algae (KITTEL and LIGOWSKI 1980). So far, it is not known whether in winter E. crystallorophias has the same access to alternate sources of food (detritus, zooplankton) as E. superba. As the former species stores wax esters, it is assumed that the animals do not feed in winter. During the last "Polarstern" expedition in October/November, E. crystallorophias were collected in open waters in large numbers. We caught many females just before spawning (blue ovaries). Towards end October, the animals had filled cardiac proventriculi [Trans.: also "crops"]and greenish mid-gut [digestive] glands. The species did not seem to occupy cracks in the ice. (108)

Inasmuch as E. crystallorophias spawns in spring (November/December) (HEMPEL et al. 1979; HEMPEL 1983; HARRINGTON and THOMAS 1987) when lipids reach their minimum, one can assume that part of the stored lipid energy was used for gonadogenesis (CLARKE 1985). On the other hand, LITTLEPAGE (1964) contends that E. crystallorophias uses its lipid stores to maintain metabolism, but not for reproduction, as he finds no increase in lipid content before the spawn. He further assumes that ova of E. crystallorophisa contain little lipid because in spring lipid stores of adults are low, but does not believe that this is detrimental because larvae in spring can use the

plentiful phytoplankton immediately. HARRINGTON and THOMAS, on the other hand, suspect that spawning in E. crystallorophias may be associated with major losses of lipids -- close to the 54% losses which CLARKE (1980) found in E. superba. They deduce this from the fact that the eggs of the neritic species, E. crystallorophias, remain suspended in the water, while those of E. superba sink. According to HARRINGTON and THOMAS (1987) the low density is due to the high wax ester content of the eggs, but there are no lipid data extant to support this view. These authors also discuss the fact that nauplia and metanauplia of E. crystallorophias do not go through the energy consuming ascent from depth to surface, which E. superba individuals make. This, however, supports the view of LITTLEPAGE (1964) that ova of E. crystallorophias are poor in lipids. E. superba repeatedly spawns hundreds to thousands of eggs (BARGMANN 1945; MAUCHLINE and FISHER 1969; EVERSON 1977; SIEGEL 1986; ROSS and QUETIN 1986). E. crystallorophias, on the other hand, seems to spawn only a few hundred eggs over a short period (laboratory studies of HARRINGTON and THOMAS 1987), so that overall expenditure of spawning energy is comparatively much lower.

There are so few lipid data available concerning Th. macrura that nothing can be said about seasonal changes of lipid content in that species. CLARKE (1984a) found high lipid contents in Thysanoessa taken end January off South Georgia (14-15% wet weight [w.w.]). Animals caught early March in the southern Scotia Sea had a lipid content of 3-5% w.w. (approximately 15-25% d.w.). REINHARDT and VAN VLEET (1986) found lipid content in a sample from Bransfield Strait

to be 4% w.w., or 60% d.w. (a most unusual relationship between wet and dry weights; one usually assumes a water content of 80%, so that lipid content ratios are % w.w.:% d.w = 1:5).

Our data for Th. macrura span the time period from October to February and display a clear seasonal trend during spring/summer, but it must be remembered that the samples did not all come from the same region: end October/beginning November, animals (11-20 mm) hauled off the Antarctic Peninsula had a lipid content averaging 10% d.w.; by (109)
mid-January, in the same area, this had increased to 30% d.w. (length 15-24 mm). Organisms from the southern Weddell Sea (11-27 mm) taken between end January/beginning February had an average lipid content of 37% d.w.. It is difficult to interpret the heterogeneous data from other workers, but the lipid contents measured in this study resemble those found by LITTLEPAGE (1964) in E. crystallorophias. Th. macrura remains smaller than E.crystallorophias, is not neritic, and has its centre of distribution further into the subantarctic regions. Furthermore, its larvae hatch, as do those of E. superba, at great depths, while E. crystallorophias larvae hatch in surface waters (MAKAROV 1979b; HARRINGTON and THOMAS 1987). Th. macrura is an omnivore like E. crystallorophias (MAYZAUD et al. 1985; HOPKINS 1985, 1987) and stores wax esters and phosphatidylcholine. The species spawns even before E. crystallorophias, from September to November (MAKAROV 1979b). Storage of wax esters suggests a prolonged phase of starvation and the above data strongly imply lipid accumulation as an energy reserve for winter. One must therefore assume that both Th. macrura and E. crystallorophias use their lipid reserves (wax esters,

phospholipids) in use them in winter and for gonadogenesis before the phytoplankton bloom; neither species was seen under the ice. It is doubtful that these two species have access to other sources of food (detritus, zooplankton). It may be that our winter samples will provide some information.

Seasonal lipid use in the Euphausiacea, Thysanoessa inermis and Th. raschi from the subarctic Balsfjords is well understood (HOPKINS et al. 1984b, 1985). Th. raschi has little lipid, stores triglycerides mainly, and in winter feeds apparently on zooplankton and detritus, rather than phytoplankton. Th. inermis, on the other hand, is rich in lipids and wax esters and lives in winter only on its energy reserves which are sufficient to fuel gonadogenesis before the onset of the phytoplankton bloom. Thus, the arctic species Th. inermis follows the same scheme of lipid use as we postulate her for the antarctic Th. macrura.

Summary and Conclusions

Much as the early developmental stages of the copepods, those of the Euphausia species -- and presumably also Thysanoessa -- will have consumed their yolk stores by calyptopis I. At this critical, first feeding stage, the animals must quickly encounter adequate feeding conditions, after which they accumulate considerable amounts of lipid. In addition to an ontogenetically driven accumulation of lipids, there is also a seasonal increase in lipid content. But whereas E. crystallorophias and Th. macrura store phospholipids and

wax esters both for overwintering and reproduction, krill survive the antarctic winter successfully using their lipids (triglycerides, phosphatidylcholine) and eating ice algae in the cryopelagic waters.

4.3. Amphipods

We examined seven Gammaridea and six Hyperiidea species from this taxon rich in species. Subantarctic data for comparison are extant (CLARKE 1984a; REINHARDT and VAN VLEET 1986) for Eusirus propeperdentatus, Cyphocaris richardi (Gammaridae), Vibilia propinqua, Cyllopus lucasii and Themisto gaudichaudi (Hyperiidae); these agree with the trends shown by the present data. Because of the great variability of the data, however, we shall not make any detailed comparisons with data from the literature: no new insights would result. Studied for the first time were the Gammarideae Eusirus microps, Orchomene (plebs, rossi), Uristes gigas, Tryphosella cf. longitelson, Epimeriella macronyx and the Hyperiideae Hyperiella macrocephala, Hyperiella (dilatata, macronyx), Primno macropa. (110)

With the exceptions of E. microps and U. gigas (lipid content < 20% d.w.), the gammarids we examined were rich in lipids. Among Hyperiidae, relatively high lipid levels were found in P. macropa (34% d.w.) and C. lucasii (24% d.w.). According to CLARKE (1984a) this applies also to V. propinqua and Th. gaudichaudii. Amphipods are an important food source for antarctic fishes (SCHWARZBACH 1987) and are, because of their high lipid levels, a high-quality

nutrient. Amphipod lipids are mainly triglycerides, and wax esters are usually stored in lesser amounts. Only P. macropa preferentially stored wax esters (60%), but even in this species triglycerides accounted for a considerable fraction (26%) of the lipids.

As gammarids age they move to greater depths and may assume a benthic life (Orchomene). On the other hand, ANDRIASHEV (1968) writes about extremely lipid-rich gammarids of the genus Orchomenopsis, which were seen and caught in enormous numbers in the pack-ice of the Ross Sea, where they fed on ice algae. Some species, such as E. propeperdentatus go through extensive vertical migrations (ANDRES 1979); others are encounted only occasionally in the pelagic zone. As a rule, amphipods are predators or, in part, scavengers. HOPKINS (1985, 1987) classifies them as opportunists with an extremely wide spectrum of foods. Hyperiideae live strictly in the pelagic zone and are often parasites on gelatinous plankton, such as salps and medusae (HOPKINS 1985, 1987; REINHARDT and VAN VLEET 1986). This ominovrous or carnivorous life style contrasts with the large lipid stores of many amphipods because these animals can feed all year and do not depend upon the phytoplankton. On the other hand, they frequently live at considerable depths -- except, for instance, Th. gaudichaudii. It is possible that the meso- and bathypelagic zones do not assure a regular food supply (LEE et al. 1971a), so that these organisms must depend on lipid reserves to live through periods of starvation (CLARKE and HOLMES 1986). For instance, C. richardi, a species caught between 700-1900 m depth had a lipid content of 55% d.w. and was thus very lipid-rich. More than 90% of the lipids were stored

as triglycerides. The benthic species, O. plebs, can survive at least one month of starvation (RAKUSA-SUSZCZEWSKI 1982). This species feeds voraciously when food is particularly abundant (short sojourn of foods in the gut); but when food is sparse, it may remain in the gut for over a week and therfore probably be used more efficiently. Lipid content reflects the nutritional state in amphipods, and the great variability of lipid data from this group is most probably explained by differences in, and irregularity of, their food supplies. Lipid content, furthermore, can also be affected by gonadogenesis and spawning. Lipid data from Cyllopus lucasii females were very heterogeneous and did not suggest any lipid accumulations related to reproductive processes. Nor did the data support either an ontogenic or a seasonal accumulation of lipids. Presumably, lipids also serve as buoyancy devices. Unfortunately, we do not yet know enough about the biology or life history of many antarctic amphipods to enable us satisfactorily to interpret individual lipid data.

4.4 Mysidacea, Decapods

Antarctomysis ohlini was the only Mysidacea studied. Towards end October, off the Antarctic Peninsula, lipid contents of O. ohlini (from a depth of 900-1700 m) measured 17-21% d.w.. Triglycerides are the main storage form, with minor amounts of wax esters. The results agree well with those that REINHARDT and VAN VLEET (1986) found in (111)
March/April off the Antarctic Peninsula. Much heavier and larger specimens to this species were hauled during Februrary in the southern Weddell Sea (0-850 m depth). Their lipid contents vary

between 19-57% d.w., and particularly females with large brood pouches have high lipid contents (34-57%). CLARKE (1983) found that lipid content of ripe Antarctomysis females in the Ross Sea was 4.5-6.6% w.w. (about 23-33% d.w.). In animals from the Weddell Sea, the wax ester fraction grew at the expense of triglycerides with the size and lipid content of the animals, so that in large females the ratio of the two lipid classes was 1:1. The lipids of North Atlantic and North Pacific, mesopelagic Mysidaceae (Eucopia, Gnathophausia) consist primarily of wax esters (MAUCHLINE 1980). According to MORRIS and SARGENT (1973), these wax esters do not necessarily originate from the food, but may be synthesized by the animals themselves.

In A. ohlini females, lipid accumulation appears to be closely related to ripening events. There are too few data to define any seasonal trends. There are, at present, no proofs of seasonal lipid accumulation in Mysidaceae (MAUCHLINE 1980), with the exception of work by BAMSTEDT (1978) who found seasonal variations in lipid content of juvenile, male and female Boreomysis arctica off the coast of Norway. He attributes this primarily to seasonal variation in food supplies, and much less to gonadogenesis and spawning because he found little difference in chemical composition between animals with and without brood pouch. According to HOPKINS (1985, 1987), Antarctomysis is ominvorous and in the Ross Sea, its nutrition resembles that of the benthic amphipod Orchomene.

Larvae and juveniles of the only decapod species studied, Acanthephyra pelagica, from the Weddell Sea (length 15-35 mm) in summer, had lipid contents of 13% and 25% d.w. (1.2 and 4.5% w.w.). There are practically no stored lipids, and 80% of the lipids consisted of phospholipids and cholesterol. The lipid pattern shows that the animals are going through an intense growing phase and have not yet laid down significant lipid reserves. A. pelagica reaches a maximal length of 85 mm (BATE 1888 in KIRKWOOD 1984). Subantarctic males and females of this species were analyzed by CLARKE and HOLMES (1986). They found considerably higher lipid contents (7-17% w.w.) in adults, linked with clear seasonal variations, at least in females, which have higher lipid contents in winter. There appears to be a similar trend in males, but only four determinations are available. Linked with these lipid contents, which are high in comparison to those of earlier developmental stages, are major changes in lipid composition. In adults, wax esters (60-70%) absolutely predominate while phospholipids have greatly decreased. HERRING and MORRIS (1975) suspect that change in the lipid pattern is related to the migration into the depths of older stages. Adult, wax ester-rich A. pelagica from subantarctic regions have a four times higher lipid content than do conspecific specimens from the Northeast Atlantic (MORRIS 1972; HERRING 1973). CLARKE and HOLMES (1986) interpret the high lipid contents of antarctic Acanthephyra pelagica as an adaptation to seasonal changes in the food supply, which are a secondary effect of the intense seasonality of primary productivity in the South Polar Sea. Omnivorous and carnivorous mesopelagic crustaceans can survive periods of starvation by calling on their large lipid reserves.

4.5 Coelenterates (112)

The carnivorous antarctic coelenterates, Calycopsis borchgrevinki, Diphyes antarctica, Pyrostephos vanhoeffeni and one ctenophore species have high water contents (> 95%) and are characterized by very low lipid contents, even in relation to dry weight. Seasonal changes in lipid accumulation could not be demonstrated. In the hydromedusa, C. borchgrevinki from the Weddell Sea, lipid contents varied from 1.4-3.5% d.w. (0.06-0.15% w.w.). CLARKE (1984a) reports a similar value of 0.05% w.w. and finds the main lipid classes to be phospholipids, triglycerides and wax esters. The present data, however, show that as lipid content increases, triglycerides and wax esters also increase, while the phospholipid percentages greatly decrease.

The upper bell of the siphonophore, D. antarctica (November, Antarctic Peninsula) also contains little lipid (1.0% d.w.), with a high phospholipid fraction. These data agree well with analyses from March/April in the Subantarctic (CLARKE 1984a; REINHARDT and VAN VLEET 1986). Upper bells of D. antarctica from the Weddell Sea contain more lipids (1.6-3.4% d.w.); the stored lipids are variously wax esters -- according to CLARKE (1984a) probably sterol esters -- or triglycerides. The upper bells contain gonads and gastrozooids, and often also orange-coloured oil inclusions, and are therefore richer in lipids than the lower bells (0.4-0.7% d.w.).

Our study of the siphonophore P. vanhoeffeni (lipid content 1.0% d.w., 55% phospholipids) is the first such analysis.

Data concerning an unidentified ctenophore species showed it to have the highest lipid contents (0.2-0.3% w.w.; 4.5-6.3% d.w.) among the coelenterates. Storage lipids were mainly wax esters (50-60%). CLARKE (1984a), too, finds a very high wax ester fraction (47%) in an uncertainly identified ctenophore (Pleurobrachia sp.?) and in a different ctenophore (Beroe), a very high -- for coelenterates -- lipid content of 2.9% w.w., with a predominance of wax ester storage lipids. Ctenophores appear to differ from other coelenterates insofar as lipids are concerned.

Even though some oil inclusions and higher storage lipid fractions (Diphyes) could be demonstrated, the low lipid contents in the coelenterates studied (exception: ctenophores?) suggest that these animals either accumulate only sparse energy stores, or that their stores do not consist of lipids (CLARKE 1984a). MORRIS et al. (1983), on the basis of starvation experiments with a North Atlantic ctenophore species, come to the conclusion that these animals consume their proteins (gut resporption). Growth efficiency is seldom greater than 10%, because when food is sparse, up to 80% of the ingested nutrients are required for maintaining energy metabolism (REEVE et al. 1978). On the other hand, when nutritional conditions are optimal, North Atlantic ctenophores reproduce explosively (self-fertilization, high numbers of offspring, high growth potential). It is possible that fluctuations in food supply cause the frequent fluctuations of

of population size in these epipelagic plankton organisms. During the "Polarstern" winter voyage to the Weddell Sea, remarkable numbers of large ctenophores were seen under the ice (MARSCHALL 1987), where they apparently fed on krill and other organisms living in ice crevasses (see also ANDRI- ASHEV 1968). At present, however, practically nothing is known of the biology of antarctic coelenterates.

4.6 Gastropods, Cephalopods (113)

Both lipid content and composition are highly variable in the various gastropod species. The larvae of benthic Lamellariidae (Prosobranchia), not heretofore studied, are covered by a mucoid envelope that helps buoyancy (LEBOUR 1935). These animals have a rather low lipid content (3.5% d.w.), but 70% of their lipids are triglycerides, i.e. storage lipids, from which the animals can live during their pelagic phase if nutrients are lacking.

The herbivorous Thecosomatae (Pteropoda) Limacina helicina (1-5 mm) and Clio pyramidata (16-35 mm) have lipid contents of 6-21% (average 10% d.w.) and 14-19% (average 16% d.w.). PERCY and FIFE (1981) found lipid contents in Limacina ("Spiratella") helicina in the Arctic to be 18-19% d.w.. KOBAYASHI (1974) assumes that in the Arctic this filter-feeder eats phytoplankton, nanoplankton or detritus in winter because growth and gonadal ripening occur mainly in that season. The carnivorous Clione limacina (Gymnosomata), on the other hand, has a very high lipid content of 28-40% d.w. (average 37% d.w.). There are no seasonal trends apparent. These epipelagic pteropods store

their energy preferentially as triglycerides. This is particularly well marked in Clione where -- with one exception (October, Antarctic Peninsula; 65% triglycerides) -- more than 80% of the lipids are triglycerides (Clio: approx. 50%; Limacina: more variable, 20-80%). In the Subarctic and Arctic, lipid contents of Clione limacina (17-31% d.w.) fluctuate markedly (IKEDA 1972; LEE 1974b, 1975; PERCY and FIFE 1981). Phospholipids make up, respectively, 31% and 62%, triglycerides 31% and 13%, of the lipids (LEE 1974b, 1975).

Clione limacina and Spongiobranchaea australis (Gymnosomata) are particularly intersting because of their extreme specialization in their prey species. Spongiobranchaea feeds only on a few Clio species; Clione, only on certain Limacina species. LALLI (1970) and CONOVER and LALLI (1972) describe this phenomenon impressively for animals caught for laboratory experiments off Nova Scotia (bipolar species). Nutrition studies by HOPKINS (1985, 1987) in Antarctica show similar conditions involving C. limacina and S. australis with L. helicina and C. pyramidata. This specialization goes so far that even the earlier developmental stages of Clione feed exclusively on the veliger larvae of Limacina (CONOVER and LALLI 1972). Both taxa spawn simultaneously so that each Clione stage can feed on Limacinae at the same stage of development. CONOVER and LALLI (1972) discuss the advantages of this "monophagia" and postulate two "compensatory mechanisms" which would allow Clione to overcome disadvantages: (1) very high assimilation efficiency, promoting maximal utilization of the Limacina when these prey are in plentiful supply; (2) the ability to survive prolonged starvation when they are not. According

to CONOVER and LALLI (1972) Clione can survive at least four weeks without food. The authors assume from this that Clione can store large reserves of energy. LEE (1974b) confirms this by studies of Clione specimens from the Canadian coast, which survived a starvation period of three months, and during that time catabolized 85% of their lipids. The current, first, data concerning antarctic Clione limacina (lipid content 37%, of which > 80% triglycerides) show that this species amasses reserves also in the South Polar Sea.

The literature contains no data on lipids of pelagic squid from polar regions. Cephalopods are but seldomly caught in plankton nets, and even the data extant are derived from two analyses of nine juvenile specimens of the antarctic species, Galiteuthis glacialis (11-25 mm). These animals have a lipid pattern that seems to reflect their early stage of development: low lipid contents (8-11% d.w.), high phospholipid fraction and few storage lipids (primarily triglycerides). These lipid levels may be quite different from those of the adults. NASH et al. (1978), for instance, find, in adult Illex illecebrosus (Nova Scotia) that the lipid content of the whole animal is 5.6% w.w. (approx. 28% d.w.); in the mantle they find 1.5% w.w., and in the liver 11.6% w.w. Triglycerides were the principal storage lipids. (114)

G. glacialis is a species endemic to the Antarctic; adults reach a dorsal mantle length of 50 cm (McSWEENY 1971 in RODHOUSE and CLARKE 1986). This species does not require lipids for buoyancy because high concentrations of ammonium chloride dissolved in the coelomic

fluid (less dense than sea water) render the specific gravity of this cranchiid squid equal to that of surrounding sea water (DENTON et al. 1969).

4.7 Polychaetes

Lipid content in the polychaetes we studied, Vanadis antarctica and Tomopteris penteri is not high (12-17% and 9-17% d.w.). The lipids consist mainly of phospholipids and cholesterol; storage lipids are low, and are usually -- at least in Tomopteris -- wax esters. Data published by CLARKE (1984a) and REINHARDT and VAN VLEET (1986) are in good agreement with the above, except for larger triglyceride fractions given by REINHARDT and VAN VLEET (1986). In our studies, lipid content of T. carpenteri in the Weddell Sea is higher (16% d.w.) than in October/November and January, off the Antarctic Peninsula (9-10% d.w.). The data indicate that both species hardly accumulate any storage lipids. They are carnivorous and feed mainly on zooplankton (e.g. RAKUSA-SUSZCZEWSKI 1968; HOPKINS 1985), so that they probably find enough food even in winter.

4.8 Chaetognaths

The carnivorous chaetognath species Sagitta gazellae, Sagitta marri and Eukrohnia hamata have water contents of 90-95%. As the polychaetes, they have low lipid contents. The lipids of S. gazellae (4% d.w.) and S. marri (12% d.w.) are mainly phospholipids (50-60%) and cholesterol (16-26%). There are few storage lipids in

S. gazellae, and in S. marri, triglycerides and wax esters are of little significance. The lipid content (13% d.w.) of E. hamata is similar to that of S. marri but the phospholipids are clearly lower, while triglycerides and wax esters in each make up 40% of the lipids. Contrary to the Sagittae, Eukrohnia hamata usually has oil inclusions. These are probably lipid stores like the oil sacs of copepods.

Lipid data from other authors are not uniform and agree only in part with those above. REINHARDT and VAN VLEET (1986) find a very high lipid content (17% d.w.) in S. gazellae, but the composition of these lipids agrees with ours, except for higher storage lipid values. The not reliably identified Eukrohniae studied by CLARKE (1983, 1984a) had very low lipid contents, and the presence of a large free fatty acid fraction suggests autolysis.

Lipid data of S. gazellae and S. marri are similar to those of the polychaetes and one may assume that these species, too, find enough nourishment during winter and need not rely on large lipid reserves (CLARKE 1984a). REEVE et al. (1970) found in their starvation (115)
experiments that Sagitta hispida does not use lipids, but its own body proteins as sources of energy. E. hamata, on the other hand, also draws, in times of hunger, on storage lipids, though these do not compare to the large energy reserves of crustaceans. It is known that antarctic chaetognaths live at greater depths in winter (DAVID 1955, 1958). It is possible that they are thereby following their prey, for instance, copepods. Nevertheless, growth does seem to be

slowed in winter, at least in S. gazellae (DAVID 1955). In addition to his seasonal vertical migration, antarctic chaetognaths (hermaphroditic) also undertake a maturation migration (DAVID 1955; HAGEN 1985). After the animals have completed their growth phase, they migrate to great depths (> 1000 m). During that time, the gonads develop into long strands which, by spawning time, may measure 70% of total body length (S. gazellae). After the ova haven been spawned, the adults die (exception: E. hamata).

It is not known whence the animals derive the energy during their downward migration to develop such voluminous gonads with, one supposes, lipid-rich eggs. Either they accumulate large energy reserves while near the surface and after having attained full size, or they feed voraciously on zooplankton on their way down and use this food for gonadogenesis. In interpreting the lipid data of chaetognaths, the animal's biology must be considerd, because current analyses all stem from surface-dwelling specimens only (developmental stage I).

4.9 Salps

The species examined, Salpa thompsoni contains more than 95% water. The low lipid content (0.08-0.13% w.w.; 2.3-3.3% d.w.) of specimens from the Weddell Sea is identical with the values found by CLARKE (1984a) in the Subantarctic. REINHARDT and VAN VLEET (1986), however, find astonishingly high lipid contents (1% w.w; 24% d.w.). The lipids are primarily phospholipids, cholesterol and triglycerides.

REINHARDT and VAN VLEET (1986) mention extremely high triglyceride fractions, due possibly to a higher lipid content. The lipid levels suggest that phytoplankton-filtering S. thompsoni -- in opposition to many herbivorous crustaceans -- do not use lipids either as energy stores or for buoyancy [the data of REINHARDT and VAN VLEET (1986) seem to me too high for gelatinous zooplankton such as salps; this is also shown by the C/N determinations of IKEDA and MITCHELL (1982); see also REINKE (1987)]. Salps regulate density by means of ions (DENTON and SHAW 1962), so that lipids are not required for buoyancy. REINKE (1978) characterizes S. thompsoni as an opportunist which, because of its high filtering rate, can survive in oligotrophic waters. On the other hand, phytoplankton blooms can be particularly well exploited by extremely rapid growth rates and short generationals cycle. The result of this can be enormous aggregations of salps (according to PIATKOWSKI [1987], to a max. 0.8 indiv./m^3). S. thompsoni overwinter is the oozooid stage, i.e. as solitary individuals (FOXTON 1966). During this phytoplankton-poor period, the number of salps is much reduced, but with the spring phytoplankton bloom, they explosively multiply vegetatively (blastozooids). For this, lipids seem to be of little importance in the salp's survival.

4.10 Fish Larvae and Young Fishes (116)

We investigated the antarctic fishes, Notothenia larseni, Trematomus eulepidotus and Pleuragramma antarcticum. Postlarvae 15-20 mm) mm) of N. larseni, for which no lipid studies were extant, have a low lipid content (13% d.w.), and high phospholipid and cholesterol

fractions (50% and 15%). Dominant storage lipids are triglycerides (24%). The young postlarvae (age class 0) are undergoing an intense growth phase, during which they are building up particularly proteins. In addition to the large fraction of structural lipids, triglycerides provide a small energy buffer for periods of starvation. Larvae and postlarvae feed mainly on small copepods and copepod ova (KELLERMANN 1986), i.e. a fairly lipid-rich food which should favour growth.

A quite different picture was seen with young fish of T. eulepidotus from the Weddell Sea caught end February. At 5 cm in length, they belong to age class 1 and have much higher lipid contents (30% d.w.). This is accompanied by by a definite increase in the storage lipid fraction. Triglycerides make up nearly 70% of the lipids. The lipid analyses suggest good feeding conditions. EKAU (1987) interprets the morphometric characteristics of T. eulepidotus, considered demersal, as indicative of the animal's occasional pelagic life. This is supported by its food of Euphausiaceae (SCHWARZBACH 1987; WÖHRMANN pers. comm.). High lipid content presumably partly compensates for absence of a swim bladder and makes pelagic life easier for these fish. In addition, the lipids are an important source of energy when feeding is poor (see also DE VRIES 1978; EASTMAN and DE VRIES 1981, 1982).

The only truly pelagic fish in the Antarctic is P. antarcticum, which dominates the piscine fauna of the High Arctic. In the Weddell Sea it represents, among larvae and adults, over 90% of individuals and biomass (HUBOLD 1984; HUBOLD and EKAU 1987). Both postlarvae and young fish 15-70 mm in length (age class 0-2, HUBOLD 1985) were

studied. Young postlarvae have low lipid contents (14% d.w.), with high phospholipid and minor triglyceride fractions. This pattern is very similar to that of N. larseni, and may be typical of fish larvae generally. Corresponding values were also found by TOCHER et al. (1985) in young herring larvae. REINHARDT and VAN VLEET analyzed Pleuragramma larvae (length not given) from the area of the Antarctic Peninsula and found a lipid content of 12% d.w.. Among the lipid classes they found 40% hydrocarbons, an unusual value, and one not supported by our results. It is likely that the specimen was contaminated. When P. antarcticum reaches 3 cm (age class 0-1) the lipid pattern changes appreciably: lipid contents increase with the size of the animal to a maximum above 40% d.w. and in conjunction with them, particularly storage lipids (triglycerides, max > 80%). At this relatively advanced stage of development, the lipid data approximate those of T. eulepidotus. When Pleuragramma reaches 4-5 cm in length, it starts to accumulate considerable quantities of storage lipids (triglycerides) in oil sacs which can be seen macroscopically in young fish (DE VRIES and EASTMAN 1978; HUBOLD pers. comm.). In the older Pleuragramma, REINHARDT and VAN VLEET (1986) find a lipid content of 48% d.w.; WILLIAMS (pers. comm. in DE VRIES and EASTMAN 1978) measures lipid content of muscle tissue at 39% d.w.. REINHARDT and VAN VLEET (1986) and DE VRIES and EASTMAN (1978) find triglycerides as storage lipids which are mainly accumulated in intestines and oil sacs. Muscle tissue contains triglycerides and wax esters in equal amounts (REINHARDT and VAN VLEET 1986).

DE VRIES and EASTMAN (1978, 1981) describe the various adaptations of

P. antarcticum, which lacks a swim bladder: in addition to reduced ossification and scales, they find that high lipid content is primarily responsible for the nearly total "weightlessness" of this pelagic species. Ossification/scale development and lipid deposition are chronologically linked in such a way that increases in density are compensated (DE VRIES and EASTMAN 1978). These authors believe that oil sacs are discrete "buoyancy devices", from which oil can not be mobilized, and which serve exclusively to reduce density. Should this hypothesis be substantiated, it would describe an unusual mechanism: either P. antarcticum does not encounter unfavourable feeding conditions, or even during times of starvation, the buoyancy provided by the oil sacs must be maintained.

4.11 Summary and Prospects

This study has shown that lipids play a central role in the life of antarctic herbivorous zooplankton (excluding salps). The nutrients ingested during the short phytoplankton bloom are stored as lipids for reserve energy and buoyancy. Thus, lipids help to compensate for the extreme seasonality of primary production because for long periods they preserve in the pelagic zone energy amassed by primary productivity. Crustacea, the major component of antarctic plankton, in particular, are characterized by an abundance of lipids, such as is not found in temperate or tropical regions. Early developmental stages of these plankton organisms often go through critical periods, when they consume most of their endogenous lipid reserves. As growth continues, they accumulate -- usually in conjunction with a phytoplankton

bloom -- immense amounts of lipids which these species use for over-wintering and reproduction. This lipid-rich zooplankton, in turn, serves higher trophic levels in the food chain (fishes, penguins, seals, whales, etc...). Without such highly nutritious plankton food, warm blooded animals would find it much harder to build-up their often enormous fat layers during the summer feeding phase. This blubber helps the animals survive either the harshness of antarctic winter or a winter migration to the oligotrophic tropics; it is also of major assistance to animals in the energy-sapping production and nurturing of offspring. Lipid accumulation by herbivores therewith assumes major importance for the entire antarctic pelagic zone.

This lipid census of antarctic zooplankton in spring and summer was designed to compare the significance of this energy-rich group of substances among different taxa, species and developmental stages. In the process, many new questions emerged, often concerned with survival of planktonic organisms in winter, and unanswerable at present because of lack of winter specimens. During the "winter Weddell Sea experiments", however, much plankton material -- comparable to summer samples -- was collected and will be studied for the relevant lipids in 1988 in order better to understand seasonality of lipid storage in the various species. It is also planned to analyze fatty acid spectra of planktonic lipids in order to identify "marker lipids" of use in the study of the trophic structure of the antarctic pelagic region. It may be assumed that seasonal differences in the pattern of fatty acids will identify seasonal shifts in food spectra.

Evaluation of this unique collection of samples should help to answer questions concerning overwintering of various plankton species, and thereby to expand our understanding of the antarctic ecosystem.

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